AGRICULTURE ET BIODIVERSITÉ : APPROCHE PLURI-ÉCHELLE DE L'ÉVOLUTION D'UNE COMMUNAUTÉ DE PETITS MAMMIFÈRES ET DE DEUX RAPACES PRÉDATEURS LE LONG D'UN GRADIENT DE PAYSAGES AGRICOLES CONTRASTÉS

Nadia Michel

No ordre : 3323

THÈSE

Présentée

DEVANT L'UNIVERSITÉ DE RENNES 1

pour obtenir

le grade de DOCTEUR DE L'UNIVERSITÉ DE RENNES 1
Mention BIOLOGIE

PAR
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Soutenue le 14 Février 2006 devant la commission d'examen

Composition du jury :

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Patrick GIRAUDOUX	Professeur, Univ. Franche-Comté	Rapporteur
Thierry TATONI	Professeur, Univ. Aix-Marseille III	Examinateur
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SOMMAIRE

INTRODUCTION

INTRODUCTION

1. La biodiversité : un concept complexe :

Le terme de biodiversité a fait l'objet de nombreuses définitions. D'après Gaston (1996), trois grands points de vue sur la diversité biologique ou biodiversité peuvent être considérés :

- la biodiversité comme un concept, exprimée de manière générale par la « variété du vivant » (nous tacherons d'en donner une définition, particulièrement basée sur les travaux de Noss (1990)).

- la biodiversité comme une entité mesurable. Dans les sciences écologiques, l'utilisation du terme « diversité » a été un précurseur à l'utilisation du terme actuel « biodiversité » . Le terme de « diversité » a donc des fondements scientifiques et est régi par des règles dérivées des théories de l'information (Shannon, 1948 ; Shannon et Weaver, 1963). Ainsi des indices ont émergé, combinant la richesse spécifique avec une mesure d'équitabilité (*evenness*) des abondances relatives des espèces.

- la biodiversité comme instrument social et politique, largement répandu par les media. Dans ce cas, ces « utilisateurs secondaires » comme les politiciens ou d'autres branches de la société n'appartenant pas aux sciences écologiques utilisent le terme biodiversité comme une valeur, synonyme de « conservation de la nature » (Bowman, 1993).

Longtemps en écologie, l'utilisation commune s'est souvent limitée au seul nombre d'éléments différents (le plus souvent nombre d'espèces, malgré la relative difficulté de cadrer la notion d'espèce) sous-tendue par l'interprétation « the-more-the-better » (Buchs 2003). En effet, en pratique, dans la majorité des cas, les espèces sont les « unités de la biodiversité » (Claridge et al. 1997). Mais comme Huston (1994) le rapporte, la biodiversité présente d'autres éléments que le simple nombre d'espèces. Quelles espèces sont présentes ? Quelles espèces sont les plus abondantes ? Quels sont leurs rôles dans le fonctionnement des écosystèmes ? Autant d'aspects importants de la diversité biologique qui ne peuvent pas être résumés dans une simple valeur. Dans le passé, la controverse autour de la quantification de la diversité a tenu dans le fait qu'on attendait beaucoup (et à tort) d'une seule mesure qu'on

espérait contenir toute l'information sur les assemblages d'espèces. Cette attente n'était clairement pas réaliste (Jeanneret et al., 2003).

Les études sur la biodiversité se sont donc focalisées pendant des années sur certains niveaux d'organisation du vivant, à savoir les espèces (ESA, 1973) et les populations (Rojas, 1992). D'ailleurs la majorité des études sur les plans de conservation sont faites en identifiant les menaces à l'échelle de l'espèce (Master, 1991 ; Rebelo, 1992 ; Sisk et al. 1994 ; Flather et al., 1998). Mais compte tenu de la complexité de la biodiversité, d'autres éléments (assemblages d'espèces, types d'habitats…) ont aussi été pris en compte (Noss et al., 1997). Ainsi d'autres études se sont intéressées non plus seulement aux taxons menacés, mais aussi aux écosystèmes menacés (Beissinger et al., 1996), aux habitat naturels et à leur statut de protection (Dinerstein and Wikramanayake, 1993) à l'endémisme et à la vulnérabilité dans les 'hotspots' (Myers, 1988 ; Mittermeier et al., 1998) ou encore à la préservation de plusieurs types d'habitat (Pressley et al., 1996). C'est ainsi que des interprétations plus récentes du terme biodiversité ne sont pas seulement restreintes à la richesse spécifique mais sont aussi reliées aux variétés, aux races, aux formes de vie et aux génotypes ainsi qu'aux unités paysagères, aux types d'habitats, aux éléments structurels, aux cultures et à la diversité de l'utilisation des terres, etc (Noss, 1990).

La définition de la biodiversité donnée par la Convention Internationale de la Diversité Biologique de la Conférence des Nations Unies sur l'Environnement et le Développement de Rio (1992) englobe la diversité génétique, la diversité des espèces et la diversité des écosystèmes (Johnson, 1993). Ainsi, le terme générique de biodiversité forme un système hiérarchique pertinent pour différentes échelles de perception (génome, population, communauté, écosystème, paysage) et pour différentes fonctions (Noss, 1990). Noss (1990) propose ainsi une définition hiérarchique de la biodiversité, articulée autour de trois attributs fondamentaux mis en évidence par Franklin et al. (1981), composition, structure et fonction (Figure A) :

« *Biodiversity is not simply the number of genes, species, ecosystems, or any other group of things in a defined area...More useful than a definition, perhaps, would be a characterization of biodiversity that identifies the major components at several levels of organization ... Composition, structure, and function ... determine, and in fact constitute, the biodiversity of an area. Composition has to do with the identity and variety of elements in a collection, and includes species lists and measures of species diversity and genetic diversity. Structure is the physical organization or pattern of a system, from habitat complexity as measured within communities to the pattern of patches and other elements at a landscape scale. Function*

involves ecological and evolutionary processes, including gene flow, disturbances, and nutrient cycling ».

Ce système hiérarchisé implique des interactions entre les différents composants. Ainsi, la qualité et/ou la quantité d'un composant de plus haut niveau a un effet direct sur la qualité et/ou la quantité d'un composant de niveau plus bas (Waldhardt et Otte, 2000). Par exemple, un changement dans la structure du paysage (composant structurel) peut résulter d'un changement d'utilisation des terres (composant fonctionnel) et affecter la composition spécifique (composant compositionnel) et au final affecter des processus écologiques (composant fonctionnel).

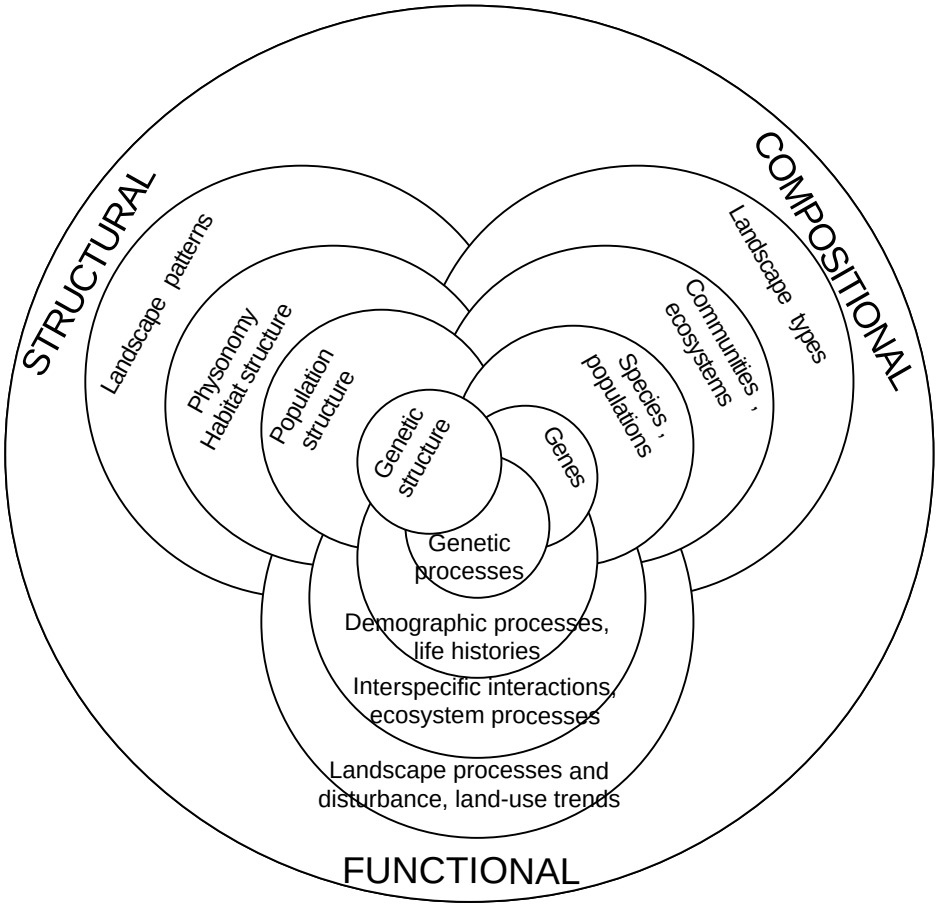


Figure A. Représentation hiérarchisée des composants Structurel, Fonctionnel et Compositionnel de la biodiversité selon Noss (1990).

2. Agriculture et biodiversité :

2.1. L'évolution récente de l'agriculture :

L'expansion des terres agricoles est largement reconnue comme étant la plus importante modification de l'environnement global par l'homme (Matson et al. 1997). La surface total de terres cultivées dans le monde entier a été multiplié par 466% de 1700 à 1980 (Meyer and Turner II, 1992), et en Europe, la principale utilisation des terres est tournée vers l'agriculture (Stoate et al., 2001).

Au cours des 50 dernières années, l'agriculture a connu des modifications très importantes à l'échelle mondiale, qui ont conduit à des transformations profondes des paysages agricoles (Burel et Baudry, 1990; Turner et Meyer, 1994; Robinson et Sutherland, 2002). Le premier changement survenu a été la mécanisation accrue des exploitations ce qui a accéléré la diminution de leur nombre (- 65%) mais l'augmentation de leur taille ; la production a été multipliée par quatre (Robinson et Sutherland, 2002). La taille des parcelles a également fortement augmentée et a conduit à l'élimination de nombreuses haies plantées au cours des siècles précédents (Rackham, 1986). En France, les capitaux disponibles grâce à la PAC (Politique Agricole Commune) par exemple ont grandement contribué à cette évolution et à la perte d'un grand nombre d'éléments semi-permanents (haies, digues, bois, prairies…). De plus , les exploitations mixtes (polyculture/élevage) ont fortement diminué au profit d'exploitations spécialisées, adoptant des rotations culturales plus simples que par le passé (Canévet, 1992 ; Robinson et Sutherland, 2002).

Un autre changement majeur a été l'utilisation de plus en plus importante d'intrants chimiques (produits phytosanitaires) sur les sols agricoles (McLaughlin and Mineau, 1995) : pesticides (la France étant le plus gros consommateur européen), incluant fongicides (41%), herbicides (39%), insecticides (12%) et autres (8%) (Commission Européenne, 1999) et fertilisants ont vu leur nombre et l'étendue de leurs applications fortement augmenter. Toutefois, depuis les années 80, on constate une baisse dans l'utilisation des fertilisants inorganiques : en France, entre 1986 et 1994 la diminution a été de 10% pour les nitrates, de 20% pour les phosphates et de 13% pour le potassium (Stoate et al., 2001) mais les quantités utilisées restent élevées.

Tous ces changements majeurs liés à l'intensification de l'agriculture moderne ont conduit à une perte de diversité dans les paysages agricoles et, de façon profonde à une transformation des systèmes écologiques au niveau planétaire (Turner II et Meyer, 1994).

2.2. Les impacts de l'agriculture moderne sur la biodiversité :

L'hétérogénéité spatio-temporelle du paysage étant essentielle pour maintenir la diversité spécifique (Huston, 1995), ces perturbations liées à l'évolution de l'agriculture moderne sont considérées comme des menaces pour la biodiversité (Solbrig, 1991). De nombreux programmes de recherche ont ainsi été développés pour évaluer les impacts de l'intensification de l'agriculture sur la biodiversité dans les paysages agricoles.

La flore des paysages agricoles est fortement concentrée dans les bords de champs (Wilson et Aebischer, 1995 ; Joenje et Klein, 1994 ; De Snoo, 1997) où la biomasse, la densité et la diversité des espèces a été réduite par l'utilisation des herbicides, en particulier les herbicides non sélectifs comme le glyphosate (Chiverton et Sotherton, 1997).

Le déclin de la diversité des papillons a été mis en évidence dans toute l'Europe (Pavlicek-van Beek et al., 1989 ; Warren et Kirkland, 1997 ; Van Swaay and Warren, 1998) et a été attribué en particulier, aux changements dans les systèmes de production, à l'augmentation de la taille des parcelles et surtout à la diminution drastiques des prairies permanentes et des prairies humides (Feber et Smith, 1995 ; Oates, 1995). Dans les paysages agricoles, les papillons sont en effet pour la grande majorité restreints aux milieux herbacés, qu'ils soient linéaires (bordures de champs, haies) (Dover, 1991, 1994) ou non-linéaires (prairies) (Oates, 1995) et la diminution de ces habitats a réduit considérablement la capacité d'accueil de ces paysages agricoles pour les papillons. Les pesticides ont également une grande importance par leur effet létal direct sur un certain nombre d'invertébrés non ciblés (Rands et Sotherton, 1986 ; Feber et al., 1997). C'est le cas par exemple pour les coccinelles (Wayland, 1991), les abeilles (Grieg-Smith et al., 1995), les bourdons (Williams, 1982) ou encore les coléoptères carabiques (Purvis et Bannon, 1992).

De très nombreuses études ont montré un impact majeur des changements des pratiques sur les oiseaux qui sont de bons indicateurs de l'évolution des paysages agricoles (Ormerod et Watkinson, 2000). Ainsi, la diminution de la surface des prairies et

l'intensification de leur utilisation, en particulier pour le pâturage ont entraîné une diminution des populations d'oiseaux, tels que le râle des genêts (*Crex crex*) (Green et Stowe, 1993), le Chevalier gambette (*Tringa totanus*) (O'Brien et Smith, 1992) ou le Vanneau huppé (*Vanellus vanellus*) (Peach et al., 1994). D'une manière générale, on assiste au déclin des espèces spécialistes (forestières par exemple) et à une stabilité des généralistes (EBCC, 2003). La destruction des haies tend à défavoriser les espèces qui y nichent comme les faisans (*Phasianus colchicus*) ou les perdrix grises (*Perdrix perdrix*) (Chamberlain et al., 2000). L'usage des insecticides affecte les poussins de perdrix grise qui se nourrissent strictement d'insectes pendant leurs premières semaines de vie (Green et al., 1986). L'alouette des champs (*Alauda arvensis*) qui préfère nicher dans une végétation basse est défavorisée par la semence de blé d'hiver, trop haut au printemps pendant la période de reproduction (Wilson et al., 1997 ; Wakeham-Dawson et al., 1998). Tous ces impacts ont ainsi conduit à un déclin important des populations d'oiseaux des paysages agricoles.

Les mammifères ne sont pas épargnés par ces effets de l'agriculture moderne. La diminution de la diversité dans les paysages agricoles a été identifiée comme étant la principale cause du déclin du lièvre brun (Hutchings et Harris, 1996). Les chauve-souris ont souffert de l'élimination de nombreux sites reposoirs, de la perte de sites de nourrissage comme les haies, et également du déclin important de leurs proies, les insectes (Walsh et Harris, 1996 ; Yalden, 1999). Les petits mammifères sont aussi touchés par le déclin de la quantité de nourriture, insectes et graines (Tew, Macdonald et Rands, 1992). Ils ont aussi été particulièrement susceptibles à la mortalité directe causée par les rodenticides ou en mangeant des graines traitées aux molluscicides (Shore et al., 1997 ; McDonald et al., 1998). Et les espèces de prairies et de zones humides comme le rat des moissons ou le campagnol agreste ont souffert de la perte de tels habitats. A l'inverse, certaines espèces généralistes communes (renard, *Vulpes vulpes*; lapin, *Oryctolagus cuniculus*) ont vu leurs effectifs augmenter (Robinson et Sutherland, 2002).

3. Intérêts de l'écologie du paysage :

3.1. Le paysage : de multiples définitions :

Avant d'être objet d'étude en écologie, le paysage a été utilisé de manière très diverse dans de nombreuses disciplines : peinture, architecture, littérature, géographie… (Berdoulay et Phipps, 1985 ; Inrap, 1986).

Le paysage de l'écologue est une configuration spatiale de patchs à une échelle pertinente pour le patron ou le processus écologique que l'on veut considérer (Farina 1998). Il ne doit pas être considéré seulement comme un endroit donné, un site géographique ou une mosaïque de patchs, mais plutôt comme un contexte physique et fonctionnel dans lequel des processus écologiques ont lieu (Swanson et Sparks, 1990, Magnuson, 1990). De nombreuses définitions ont été données. Déjà il y a 200 ans, le géographe Allemand von Humboldt considérait le paysage comme « *the total character of a region* ». Et Troll (1968) parle de « *Total spatial entity of human living space* ». Plus récemment, des définitions plus précises ont été données : pour le géographe Bertrand (1975), le « *paysage est un media entre la nature et la société ayant pour base une portion d'espace matériel qui existe en tant que structure et système écologique, donc indépendamment de la perception* ». Avec l'avènement de l'écologie du paysage, dans le premier livre de cours sur la discipline, Forman et Godron (1986) écrivent qu' « *un paysage est une portion de territoire hétérogène composé d'ensembles d'écosystèmes en interaction qui se répètent de façon similaire dans l'espace* ». Burel et Baudry (2001) ont fait la synthèse de ces deux définitions données par Bertand, et Forman et Godron en définissant le paysage comme « *un niveau d'organisation des systèmes écologiques supérieur à l'écosystème ; il se caractérise essentiellement par son hétérogénéité et par sa dynamique gouvernée pour partie par les activités humaines. Il existe indépendamment de la perception*. ». C'est cette dernière définition que nous retiendrons.

3.2. L'écologie du paysage : une discipline récente :

C'est en 1939 que Troll utilise pour la première fois le terme écologie du paysage (Troll, 1939), dans le but de combiner deux disciplines : la géographie et l'écologie, et donc de relier les structures spatiales aux processus écologiques (Burel et Baudry, 2001). Mais

l'écologie du paysage n'est reconnue comme discipline à part entière par la communauté scientifique internationale que dans les années 1980 avec l'intégration de solides théories et concepts qui font de l'écologie du paysage une science écologique moderne (Forman et Godron, 1981 ; Risser et al., 1983, Forman et Godron, 1986 ; Zonneveld, 1995 ; Forman, 1995…). L'écologie géographique (MacArthur, 1972), la théorie biogéographique des îles (MacArthur et Wilson, 1967), la théorie de la percolation (Stauffer, 1985, Gardner et al., 1992), la théorie hiérarchique (Allen et Starr, 1982 ; Allen et Hoekstra, 1992), la théorie des perturbations (Pickett et White, 1985), la théorie des métapopulations (Levins, 1970 ; Gilpin et Hanski, 1991 ; Hanski et Gilpin, 1991, Hanski et al., 1994) ou encore la théorie du chaos (Gleick, 1991) sont les approches théoriques les plus pertinentes qui ont contribué à l'avènement de l'écologie du paysage.

Les principaux apports de l'écologie du paysage peuvent se résumer en trois points :

1) la prise en compte de l'hétérogénéité spatiale et temporelle des systèmes écologiques :

Jusqu'aux années 1970, les programmes de recherche en écologie se sont focalisés sur les systèmes naturels considérés comme homogènes, comme par exemple la forêt (Duvigneaud, 1980). Mais avec l'émergence de l'écologie du paysage, cette homogénéité structurelle a progressivement laissé la place à l'hétérogénéité fonctionnelle des systèmes étudiés (Lefeuvre et Barnaud, 1988). Par exemple dans un paysage agricole, la matrice, jusqu'alors homogène n'est plus considérée comme un ensemble de patchs d'un seul type représentant un environnement hostile, mais comme une mosaïque de patchs de différentes natures plus ou moins perméables aux flux et à l'accueil des espèces (Burel 1996). L'hétérogénéité du paysage devient alors un facteur pertinent pour la prédiction et l'évaluation de la biodiversité (Jeanneret et al. 2003).

2) la prise en compte des activités humaines comme partie intégrante des systèmes écologiques :

L'écologie du paysage se différencie de l'écologie classique par la prise en compte non seulement des écosystèmes mais aussi des activités humaines qui agissent sur la dynamique de ces écosystèmes. Ainsi, le paysage est la résultante d'une confrontation continue entre la société et son milieu (Burel et Baudry, 2001). La prise en compte de l'action anthropique sur le paysage et sur les processus écologiques est d'autant plus pertinente à notre époque où l'emprise de l'homme est de plus en plus importante (croissance démographique, industrialisation, développements technologiques), affectant l'ensemble des paysages et des

écosystèmes de la planète de façon directe par une exploitation des ressources et une occupation accrue de l'espace (agriculture, urbanisation), ou de façon indirecte par les changements climatiques globaux ou les pollutions induites par le développement de l'industrie (Burel et Baudry, 2001).

3) la prise en compte de l'espace et du temps de façon explicite

En effet, la spatialisation des données, et en particulier la prise en compte de l'hétérogénéité spatiale comme on l'a vu plus haut, de même que la prise en compte de l'hétérogénéité temporelle, c'est-à-dire de l'histoire, récente ou ancienne des paysages, permettent une meilleure compréhension des processus écologiques et des mécanismes évolutifs des paysages (Burel et Baudry, 2001).

3.3. L'intérêt des habitats (semi-)permanents comme objet d'étude :

Avec l'émergence des principes de l'écologie du paysage et l'intérêt croissant pour l'étude des paysages anthropisés, dont font partie les paysages agricoles, une attention toute particulière a été portée sur l'étude de la composition, de la structure, et du fonctionnement des habitats (semi-) permanents (bois, bords de champs, haies, prairies permanentes) dans la mosaique des paysages agricoles (Forman, 1995 ; Marshall et Arnold, 1995 ; Kleijn et Verbeek, 2000 ; Freemark et al., 2002). Parmi ces éléments semi-permanents, les haies (ou bandes de végétation arborescente qui séparent des champs adjacents), occupent une place importante (Forman et Baudry, 1984 ; Baudry et al., 2000). En plus d'une reconnaissance de leurs fonctions traditionnelles, telles que limites de parcelles ou de propriété, barrières, source de bois, protection contre le vent, mais aussi protection contre l'érosion (Burel et Baudry, 1990 ; Cherrill, 1996 ; Baudry et al., 2000), les haies sont de plus en plus reconnues comme ayant un rôle majeur dans le maintien de la diversité biologique dans les paysages agricoles (de Blois et al., 2002).

En effet, ces éléments linéaires semi-naturels se rencontrent dans de très nombreux paysages agricoles dans le monde entier, et ont une place centrale comme refuge de la biodiversité rurale, en abritant un très grand nombre d'espèces animales et végétales (Dover and sparks, 2000 ; Hinsley and Bellamy, 2000 ; French and Cummins, 2001 ; Tattersall et al., 2002 ; Freemark et al., 2002). De plus elles servent également très souvent de corridors pour

la migration des espèces entre patchs d'habitats favorables dans des paysages fragmentés (par exemple le mouvement d'espèces forestières entre 2 bois isolés) (Burel et Baudry, 1994 ; Forman, 1995 ; Tischendorf et al., 1998 ; Corbit et al., 1999).

Pour de nombreuses espèces de petits mammifères (à l'exception des espèces strictement prairiales), les haies constituent un élément important du paysage agricole puisqu'elles constituent un habitat permanent, bien que des excursions de recherche de nourriture dans les champs cultivés adjacents soient envisageable lorsque le couvert est suffisant (Burel 1996).

4. Problématique de la thèse :

4.1. Intérêt du modèle biologique : les petits mammifères :

Les petits mammifères sont assez peu utilisés comme modèle dans les études sur la biodiversité car ils sont souvent considérés comme des organismes ravageurs des cultures et sont donc plutôt étudiés en tant que tels (Delattre et al., 1999 ; Hansson, 1989). Cependant, ce groupe taxonomique constitue un modèle biologique de choix pour les études à l'échelle du paysage grâce à l'importance de leur rôle dans le fonctionnement des écosystèmes (Ryskowski, 1982 ; Shvarts et al., 1997). Ils constituent en effet une communauté clé dans divers processus écologiques. Ce sont des consommateurs, granivores, herbivores et insectivores. Ils participent à la dispersion et à l'enfouissement des graines. Ce sont des fouisseurs, qui participent à la décomposition de la matière organique du sol. Ce sont des hôtes, vecteurs d'un certain nombre de maladies et de parasites (exemple : l'échinococcose alvéolaire) (Delattre et al., 1985). Enfin, et surtout, ils constituent, en tant que proies, la base de l'alimentation d'un grand nombre de prédateurs, mammifères ou oiseaux. Ils peuvent donc influencer directement l'abondance et la diversité de ces prédateurs (Butet et Leroux, 1993, 2001 ; Salamolard et al., 2000). De plus, ce sont les Vertébrés les plus « facilement » capturable, à des densités suffisantes pour permettre des analyses statistiques robustes et se sont également les Vertébrés dont la biologie est la mieux connue (Barret et Peles, 1999).

⇨ **Le rôle clé de la communauté de petits mammifères dans les écosystèmes en fait un modèle biologique de choix comme indicateur de biodiversité dans les paysages agricoles.**

4.2. Problématique et plan de la thèse :

Ce travail s'inscrit dans une problématique commune à l'équipe Écologie du paysage de l'UMR 6553 ECOBIO et de l'INRA SAD de Rennes, sur les relations entre agriculture et biodiversité. Cette collaboration a permis la mise en place, au sein du site Atelier de Pleine-Fougères (Zone Atelier « Bretagne continentale »), de sites d'observations communs et d'études pluridisciplinaires à long terme sur la dynamique des paysages agricoles (bocages, agriculture intensive) et leurs conséquences sur différents modèles biologiques, animaux ou végétaux. Pour étudier la relation entre agriculture et biodiversité, l'idéal serait de disposer de données d'abondance et de diversité des taxons étudiés sur de nombreuses années, pour mettre en relation une évolution temporelle de l'agriculture et de la biodiversité. Mais de telles études sont très difficiles à entreprendre. D'où l'intérêt d'un site d'étude comme le site atelier de Pleine-Fougères où nous disposons d'unités paysagères très proches géographiquement, mais très contrastées du point de vue de l'agriculture et des caractéristiques paysagères. On fait donc l'hypothèse que ces différences vont permettre de mettre en évidence un « effet paysage » sur les communautés.

Cette thèse s'inscrit également dans le cadre du programme de recherche national « ECCO » (Ecosphère Continentale : Processus et modélisation), sur l'action thématique « Fonctionnement et Dynamique de la Biosphère Continentale : processus, échanges de matières et d'énergie, modélisation [PNBC] ». L'objectif de ce programme est de comprendre comment s'articulent la structure des paysages (en lien direct avec les activités humaines), la qualité de leurs éléments et les dynamiques écologiques pour prédire les impacts des changements des activités sur les fonctionnements écologiques. Le projet porté par l'équipe Écologie du paysage s'intéresse plus particulièrement aux conséquences de l'intensification agricole sur l'architecture des réseaux trophiques et les transferts de biomasse dans un modèle proies - prédateurs (petits mammifères, rapaces).

L'objectif de ce travail de thèse est de décrire et tenter de comprendre les processus qui régulent l'abondance et la diversité des petits mammifères dans les réseaux de haies des paysages agricoles, ainsi que leur dynamique saisonnière. Une partie traite également des conséquences de la composition du paysage et de la disponibilité en proies sur deux espèces de rapaces prédateurs des petits mammifères.

La thèse est construite sur la base d'articles scientifiques, précédés par une présentation des sites et des stations d'étude, et complétés par une synthèse qui met en lumière les principaux résultats obtenus.

Quatre axes principaux de travail ont été considérés :

Chapitre 1 : Caractériser la structure et la composition de la communauté de petits mammifères des réseaux de haies sur un gradient de paysages agricoles contrastés, en réponse à l'intensification de l'agriculture. Les résultats sont présentés dans l'article:

« How does landscape use influence small mammal diversity, abundance, and biomass in hedgerow networks of farming landscapes ?"

(article accepté dans Acta Oecologica).

Chapitre 2 : Identifier les facteurs environnementaux responsables de la structure et de la composition des assemblages d'espèces. L'ensemble des résultats est présenté dans l'article :

« Role of habitat and landscape in structuring small mammal assemblages in hedgerow networks of contrasted farming landscapes in Brittany, France »

(article soumis à Landscape Ecology).

Chapitre 3 : Caractériser les variations saisonnières de la communauté et des populations qui la composent en réponse à la dynamique du paysage. Ces résultats sont exposés dans l'article :

« Seasonal changes in a small mammal community from hedgerows of contrasted agricultural landscapes in Western France »

(article soumis à Ecoscience).

Chapitre 4 : Evaluer l'impact de la structure du paysage et de la disponibilité en proies sur un niveau trophique supérieur : exemple de l'abondance de deux rapaces diurnes prédateurs des petits mammifères, la buse variable (*Buteo buteo*) et le faucon crécerelle (*Falco tinnunculus*). Les résultats de cette étude sont présentés dans l'article :

« Response of two diurnal raptors, the Common Buzzard (*Buteo buteo*) and the Eurasian Kestrel (*Falco tinnunculus*), to agricultural intensity in three landscape units of Western France »

(article en préparation).

Ce travail a nécessité la prise en compte de plusieurs échelles spatiales d'observations :

4) l'échelle du paysage (10 à 25 km²) : il s'agit des unités paysagères utilisées dans le cadre du site atelier de Pleine-Fougères, définies par analyses de photographies aériennes sur la base du grain de la mosaïque agricole, de la densité des réseaux de haies et de la proportion relative des prairies par rapport aux champs cultivés. L'utilisation de cette échelle a permis de tester l'hypothèse d'une réponse des assemblages d'espèces de petits mammifères et aux différents contextes paysagers d'une même région.
5) l'échelle des éléments permanents (stations d'échantillonnage) et de la mosaïque agricole qui les environne (0.3 km²) : on teste l'hypothèse que la communauté et les populations qui la composent peuvent être influencées par les caractéristiques intrinsèques des élément permanents qui constituent l'habitat, et également par la connectivité et la nature de l'occupation du sol qui les environnent.

PRÉSENTATION DES SITES ET DES STATIONS D'ÉTUDE

1. LES TROIS SITES DE L'ÉTUDE

1.1 Présentation générale :

Les trois sites, ou unités paysagères, de notre étude ont été choisies pour leur contraste en terme de caractéristiques paysagères et de production agricole.
Ces trois sites, nommés Bocage 1 (BOC1), Bocage 2 (BOC2) et Polder (POL) sont localisés dans le site Atelier de Pleine-Fougères, en Bretagne et en Normandie, dans les départements d'Ille-et-Vilaine (35) et de la Manche (50) (Figure A.1).

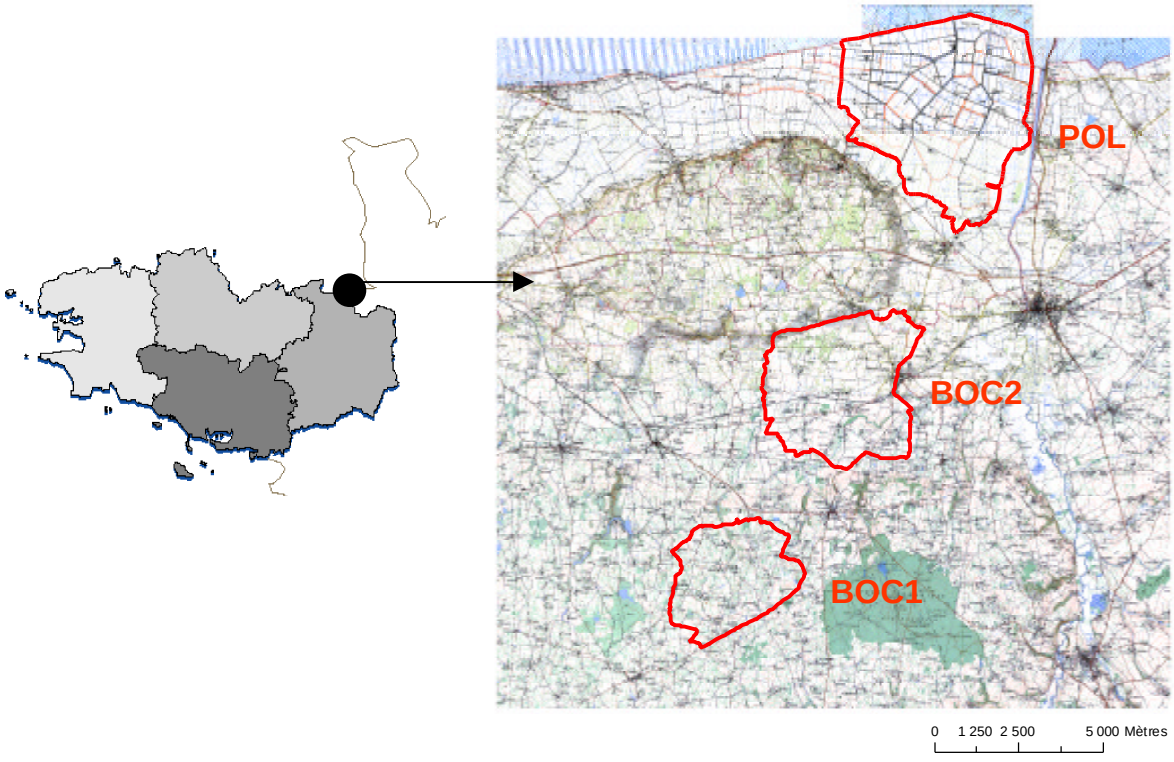


Figure A.1 Cartes de localisation des trois unités paysagères, BOC1, BOC2 et POL.

Le site BOC1 (1019 hectares) est situé principalement sur la commune de Trans-la-Forêt, le site BOC2 (1659 hectares) sur la commune de Pleine-Fougères et le site POL (2544 hectares) sur la commune de Saint-Georges de Gréhaigne.

Les deux sites bocagers présentent une histoire bien différente de celle des polders. L'embocagement commence à l'époque médiévale, au XVe siècle. On ne parle pas encore de véritable bocage et le paysage reste encore très ouvert. Entre le XVIe et le XVIIIe siècle, le réseau bocager progresse même si il n'a pas encore la densité maximale atteinte entre 1850 et 1950. En effet, au XIXe siècle, la densification du réseau est très rapide avec la conquête des landes et leur mise en culture. Au contraire, à partir des années 1960, l'arasement de nombreuses haies et la création de vastes parcelles contribuent à l'évolution rapide des structures bocagères qui régressent. Ce fut particulièrement le cas pour le site BOC2, qui a subi d'importantes opérations de remembrement depuis les années 1970 (Burel et Baudry, 2001), à l'inverse du site BOC1 dont le réseau de haies est resté très dense.

L'histoire du site des polders (POL) est très différente de celle des deux sites bocagers. En effet, les polders de la Baie du Mont Saint-Michel constituent un paysage néoformé récemment gagné sur la mer. La première expérience de poldérisation des polders remonte à la construction de la digue de la Duchesse Anne ou digue Sainte-Anne, commencée en 1054 et terminée au 16ème siècle. Puis l'effort de poldérisation a cessé pendant plusieurs siècles, et la « grande conquête » ne débuta qu'en 1851 pour s'achever en 1934 et aboutir au paysage actuel (Figure A.2) (Acx, 1991 ; Legrand, 1995) (Figure 1.2). Les polders ont aussi connu une évolution de l'occupation des sols : le site était d'abord dominé par les prairies jusque dans les années 1950, puis s'est progressivement orienté vers les cultures maraîchères et céréalières. Le réseau de digues est soit maintenu en herbe (fauche, brulis), soit plantées, le plus souvent par des peupliers. Certains tronçons de digues supportent des habitats boisés évoluant vers des haies plus traditionnelles. Ce sont ces fragments de digues boisées que nous avons pris en compte dans notre étude.

Les trois sites, très proches présentent des caractéristiques climatiques similaires (Tableau A.1).

Tableau A.1 Caractéristiques climatiques (précipitations annuelles moyennes en mm, durée annuelle moyenne d'ensoleillement en heures, températures minimales et maximales en °C) sur le site Atelier de Pleine-Fougères.

Précipitations (mm)	Ensoleillement (heures)	Température (°C)
800	1800	20-22

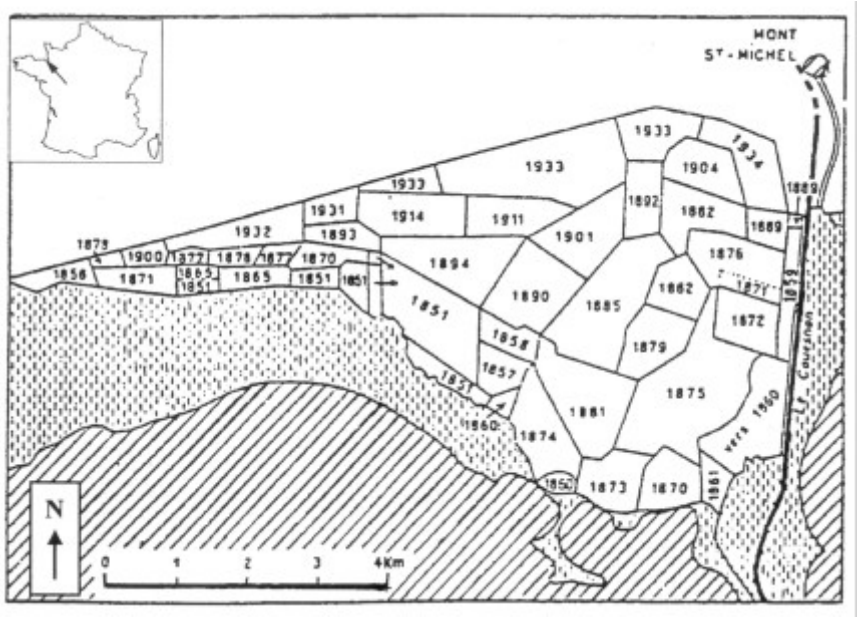


Figure A.2 Conquête progressive des polders de la Baie du Mont Saint-Michel (d'après Verger, 1968).

1.2 Cartographie :

Une cartographie des trois unités paysagères a été réalisée à partir des cartes IGN au 1/25000 et de photographies aériennes. Les cartes des sites BOC1 et BOC2 existaient déjà dans le cadre du site Atelier. En revanche, pour les Polders, la numérisation complète du site et son géoréférencement ont été nécessaires, et effectués à l'aide des logiciels ArcMap et ArcInfo. L'occupation du sol des différentes parcelles a été renseignée par relevés directs sur le terrain.

Les cartes d'assolement ainsi obtenues sont présentées Figure A.3 pour BOC1, Figure A.4 pour BOC2 et Figure A.5 pour POL, et les cartes représentant les réseaux de haies sont présentées Figure A.6.

BOC1

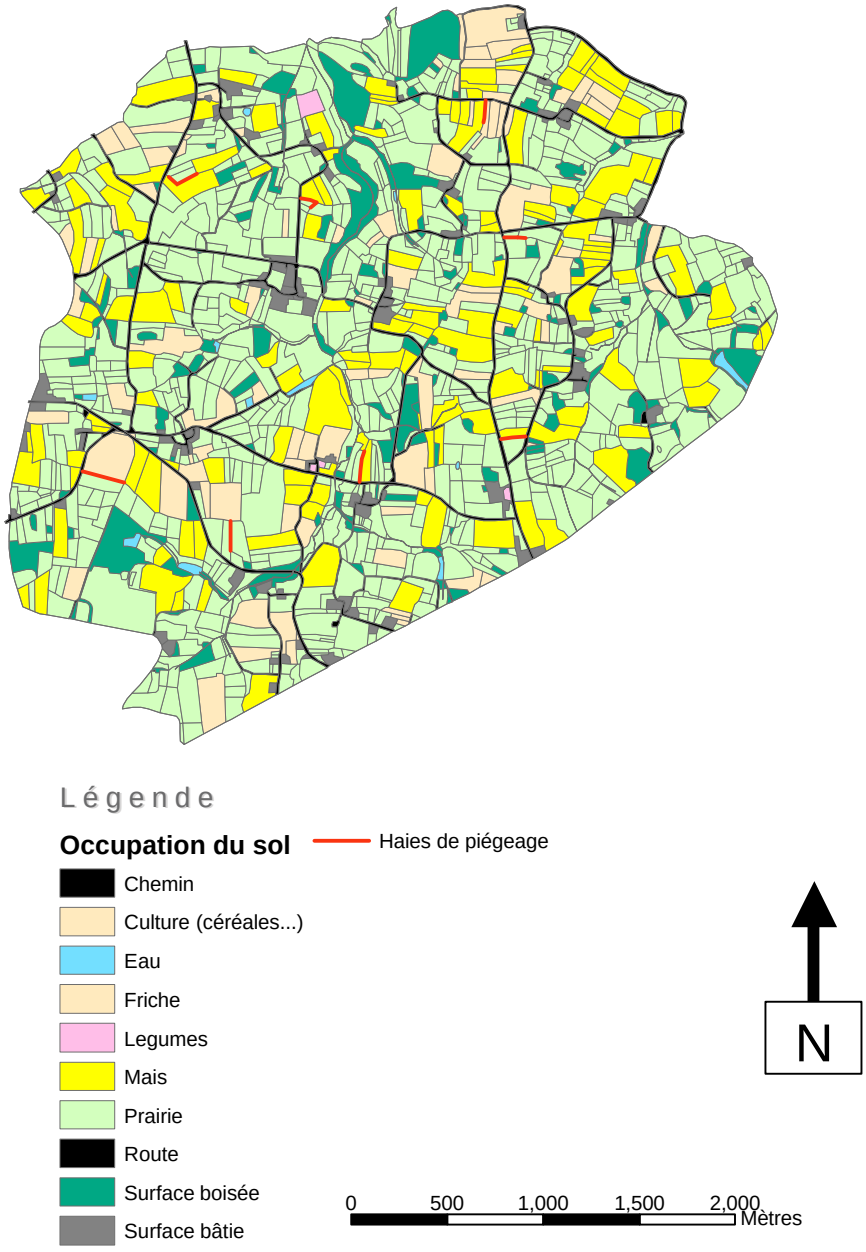


Figure A.3 Carte de l'assolement du site BOC1 en 2003.

BOC2

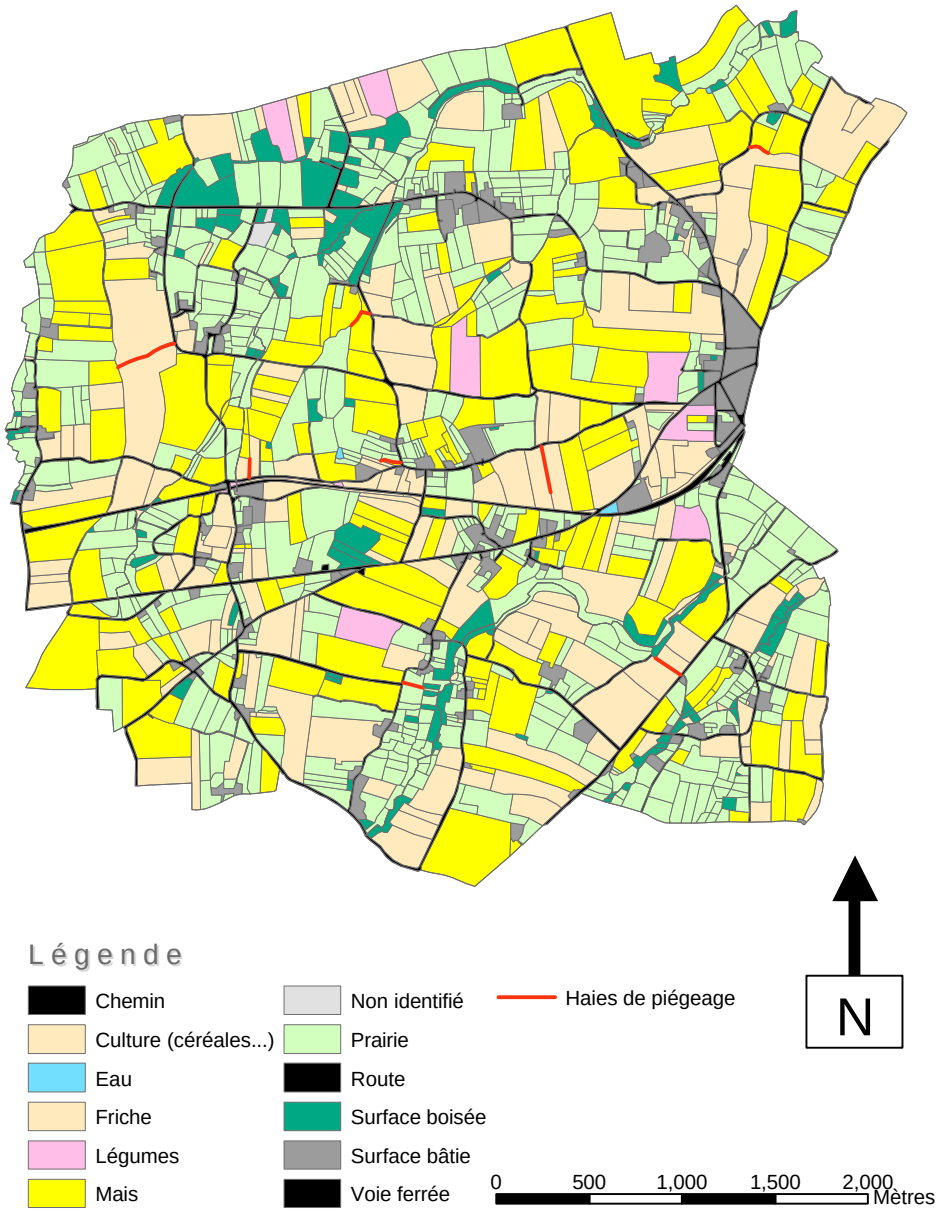


Figure A.4 Carte de l'assolement du site BOC2 en 2003.

POL

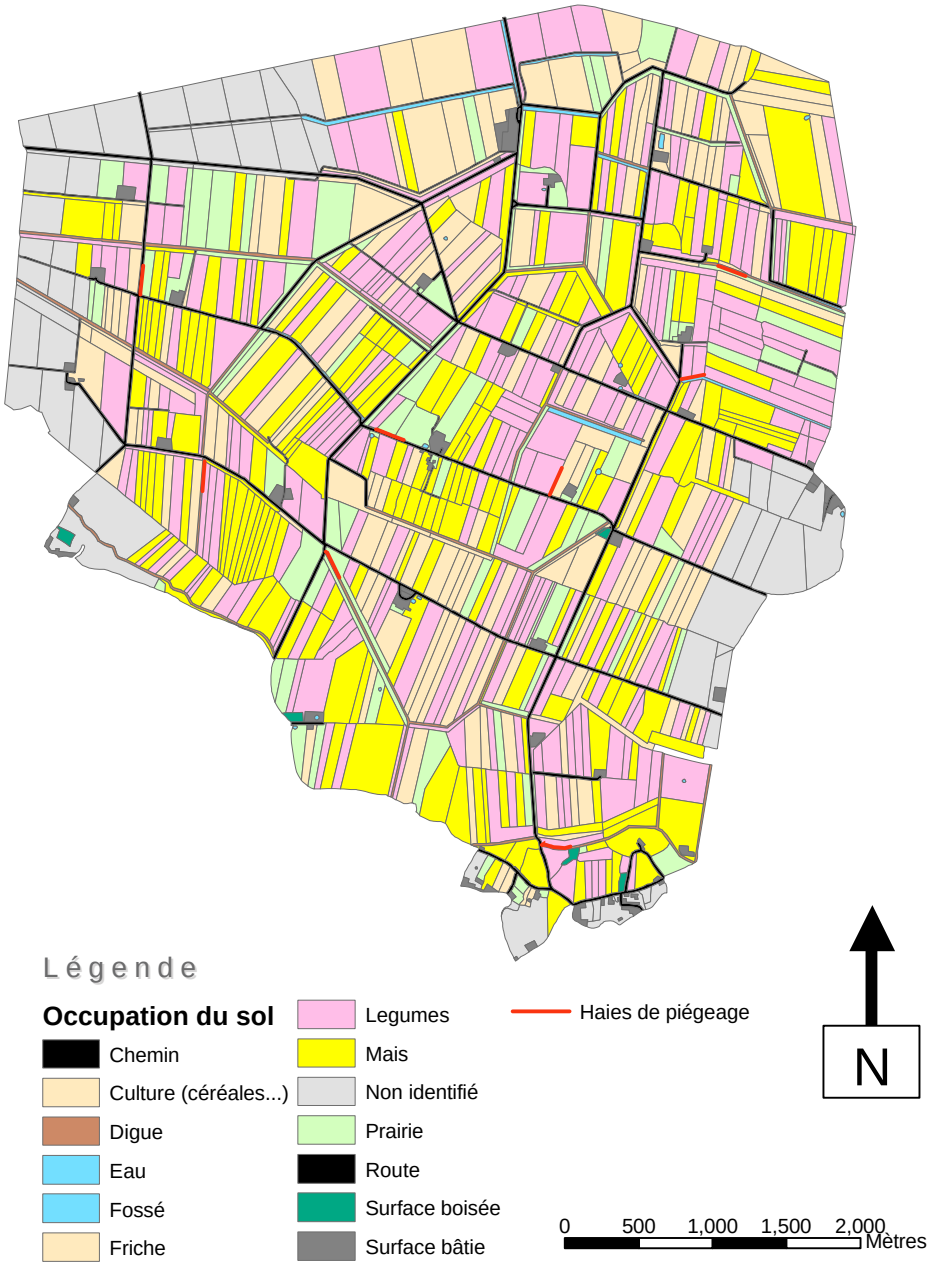
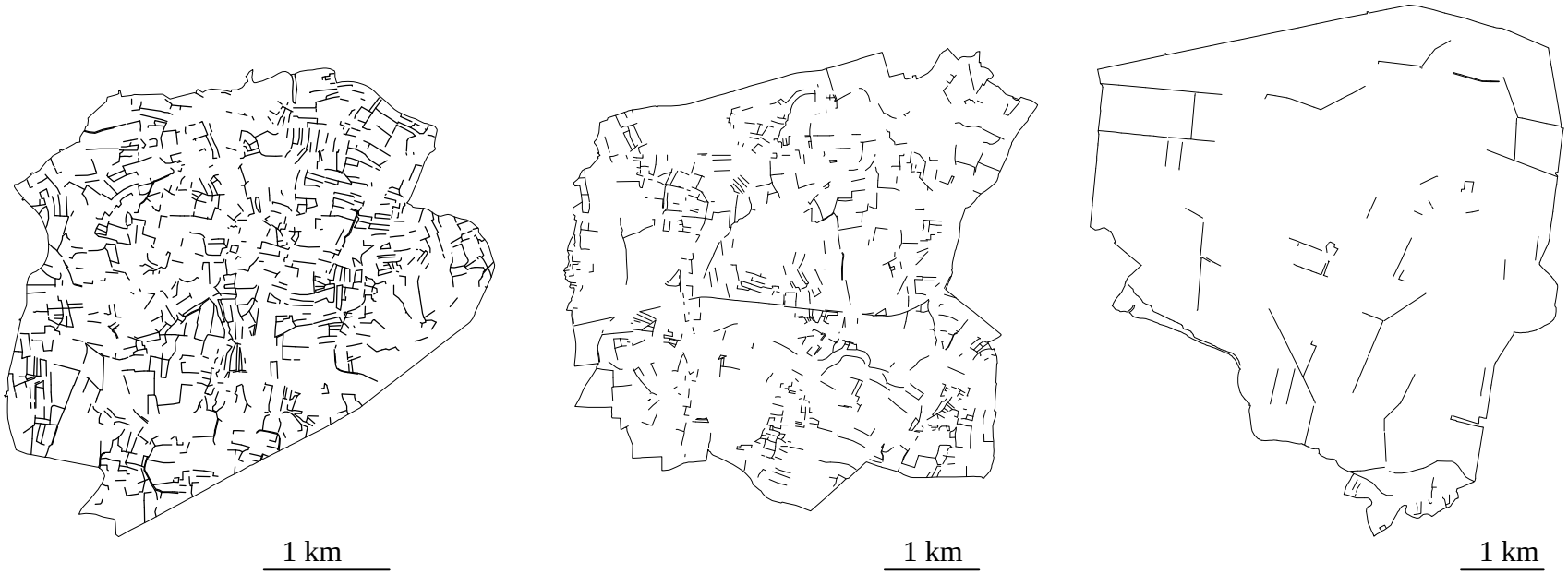


Figure A.5 Carte de l'assolement du site POL en 2003.



BOC1 BOC2 POL

Figure A.6 Cartographie du réseau de haies des trois sites.

1.3. Production agricole :

1.3.1. Orientation technico-économique :

Dans le cadre du site Atelier, un suivi régulier est effectué par l'équipe de l'INRA SAD Armorique de Rennes sur les caractéristiques de production agricole d'un certain nombre d'exploitations dans les trois sites.

La figure A.7 présente les principaux types de productions agricoles de chaque commune issus des statistiques sur les marges brutes standards des exploitations suivies par le SAD. A partir de ces données, l'OTEX (Orientation technico-économique) moyenne est déduite pour chacune des trois communes et est présentée Tableau A.2 (les codes des OTEX sont donnés en Annexe 1).

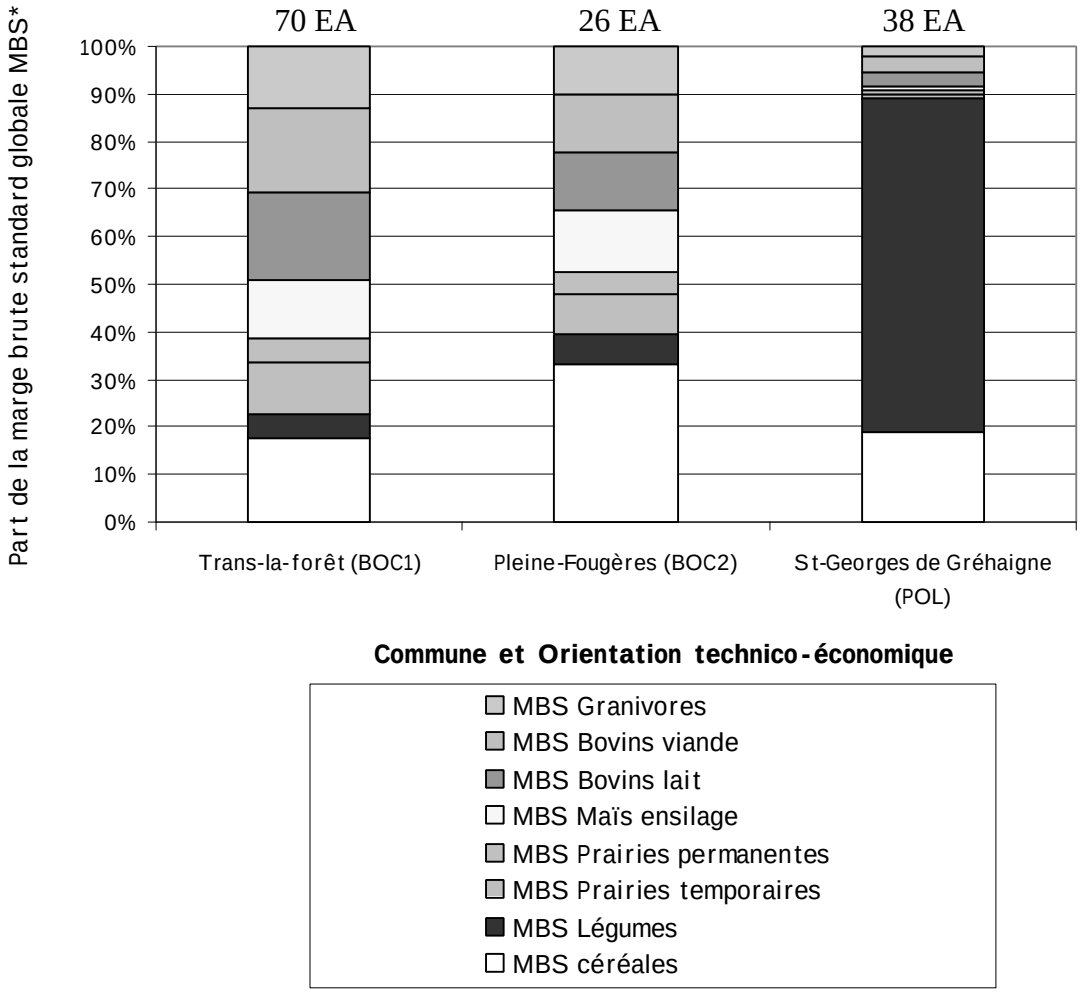


Figure A.7 Orientations technico-économiques des exploitations des trois communes, Trans-la-Forêt, Pleine-Fougères et Saint-Georges de Gréhaigne. Source : Agreste RGA 2000.
EA = Exploitation agricole ; MBS = Marge Brute Standard.

Table A.2 Orientation technico-économique moyenne des trois communes :

Commune	*OTEX moyenne*
Trans-la-Forêt	OTEX 43 : **Bovins Lait-Viande**
Pleine-Fougères	OTEX 71 : **Polyélevage à orientation herbivores**
Saint-Georges de Gréhaigne	OTEX 14 : **Cultures générales**

1.3.2. Utilisation des terres et cheptel :

Le tableau A.3 présente les pourcentages d'occupation du sol et les caractéristiques des cheptels dans les trois unités paysagères. BOC1, orienté principalement vers la production de bovins (viande et lait) (tableau A.2) se caractérise par une prédominance des prairies par rapport aux cultures (dominées par le maïs et les céréales) et a la plus faible surface moyenne des parcelles. BOC2, caractérisé par le polyélevage à orientation herbivores (tableau A.2) présente un profil d'occupation du sol inverse (dominance des cultures, maïs et céréales au détriment des prairies) et a une surface moyenne des parcelles intermédiaire. Enfin, le site POL est clairement tourné vers la culture, avec en particulier les légumes et présente la surface moyenne des parcelles la plus élevée.

Tableau A.3 Surface moyenne des parcelles, profils d'occupation du sol (proportion d'utilisation des terres pour le mais, les légumes, les céréales et la prairie) et caractéristiques du cheptel (en nombre de têtes par hectare de Surface Agricole Utilisée) pour les trois unités paysagères.

	BOC1	BOC2	POL
Surface moyenne des parcelles (ha)	0.65	1.08	2.54
Assolement			
% Prairie	**68.3**	**38,2**	**11.5**
% Cultures	**33.7**	**62**	**88.5**
- % Mais	*21.7*	*32,6*	*28.2*
- % Légumes	*0,2*	*2.1*	*35,3*
- % Céréales	*11.8*	*27.3*	*25*
Cheptel			
Bovins lait (nb/ha SAU)	0.54	0.49	0.06
Bovins viande (nb/ha SAU)	0.74	0.55	0.17
Volailles (nb/ha SAU)	16.43	12.91	15.89
Porcs (nb/ha SAU)	1.09	0.76	0

1.3.3. Réseaux de haies et bois :

La figure A.6 fait apparaître une grande disparité dans la densité des réseaux de haies des trois sites. Les linéaires de haies ainsi que les surfaces en bois sont données dans la figure A.8. On voit clairement apparaître un gradient d'ouverture du paysage du sud vers le nord : BOC1 présente un réseau de haie très dense, et une densité en bois importante, BOC2 un réseau moins dense et plus fragmenté (dû au remembrement des années 70) et enfin dans le site POL, les haies sont très clairsemées et isolées, et les bois sont presque inexistants.

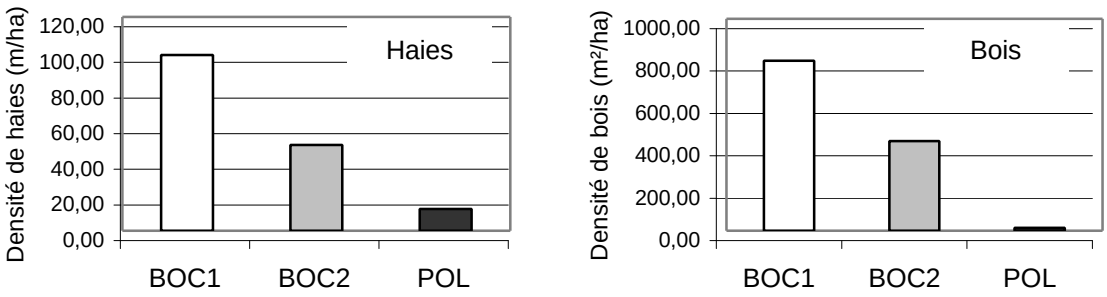


Figure A.8 Densité du réseau de haies (en m/ha) et des bois (en m²/ha) dans les trois unités paysagères.

⇨ **Les trois unités paysagères BOC1, BOC2 et POL sont caractérisées par un double gradient (du sud vers le nord) d'ouverture du paysage (diminution de la densité du réseau de haies, augmentation de la taille des parcelles) et d'intensification de l'usage des terres (éléments cultivés versus prairies).**

2. LES STATIONS DE PIEGEAGE :

Un total de 8 haies par unité paysagère ont été sélectionnées par prospection sur le terrain. Elles ont été nommées B1-1 à B1-8 pour le site BOC1, B2-1 à B2-8 pour le site BOC2 et P-1 à P-8 pour le site POL. Ces haies ont été choisies pour présenter une certaine hétérogénéité en terme de physionomie, de largeur et d'environnement paysager. L'espacement entre les haies a aussi été un critère de choix, afin d'éviter les phénomènes d'autocorrélation spatiale. Ainsi, les stations de piégeage sont au minimum distantes de 600m pour BOC1 et de 700m pour BOC2 et POL. L'accessibilité pour le travail de terrain a aussi été prise en compte. Des photographies de quelques unes des stations d'échantillonnage sont présentées Planche 1.

2.1. Structure et composition des haies :

Afin de caractériser chacune des 24 stations de piégeage, des paramètres de structure et de composition ont été relevés sur le terrain.

2.1.1. Structure :

Les mesures suivantes ont été retenues (Rq : d'autres mesures avaient été prises en compte sur le terrain mais éliminées par la suite à cause de leur non indépendance):

- Largeur
- Hauteur du talus
- Profondeur du fossé de bordure

Concernant ces trois variables, on fait l'hypothèse que des éléments de tailles différentes peuvent renfermer des abondances en petits mammifères différentes.

- Hauteur moyenne de la canopée
- Recouvrement en arbres (de 0 à 5 : 0=0%, 1=1-10%, 2=10-25%, 3=25-50%, 4=50-75%, 5= >75%)

On fait l'hypothèse que la structure de la strate arborée peut avoir une influence sur la protection vis-à-vis des prédateurs et donc agir sur les abondances d'espèces.

Planche 1. Photographies de quelques stations de piégeage (haies B1-2, B1-3, B2-2, B2-4, P-2 et P-3) (Photos : Yann Rantier).

2.1.2. Composition :

Un relevé exhaustif des espèces végétales présentes dans les trois strates (herbacée, arbustive et arborescente) a été effectué sur une longueur de 25m dans chacune des haies (Annexes 2, 3 et 4). Nous en avons déduit les richesse spécifiques de chacune des strates pour chacune des 24 stations de piégeage. On suppose que la diversité des espèces végétales sous-tend une diversité de ressources.

Les valeurs de structure et de composition des 24 haies sont données Tableau A.4.

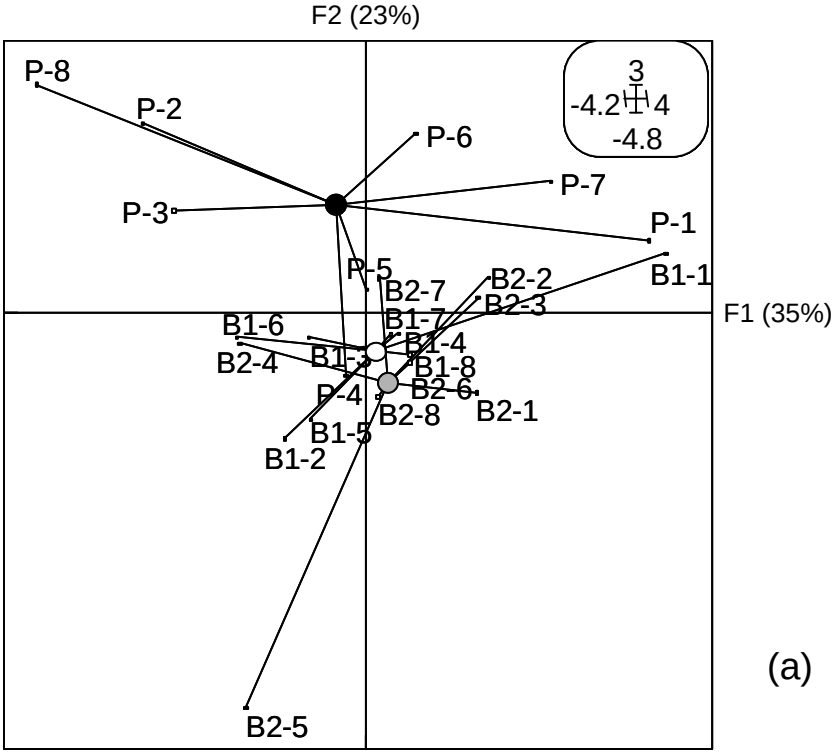
Tableau A.4 Structure et composition floristique des 24 stations de piégeage.
Structure : L=Largeur (m), HT=Hauteur du talus (m), HC=Hauteur moyenne de la canopée (m), PF=Profondeur du fossé (m), RCA=Recouvrement en arbres (de 0 à 5).
Composition : RSH=Richesse spécifique de la strate herbacée, RSU=Richesse spécifique de la strate arbustive, RSA=Richesse Spécifique de la strate arborescente.

	Structure					Composition		
Haies	**L**	**HT**	**HC**	**PF**	**RCA**	**RSH**	**RSU**	**RSA**
B1-1	2,3	0,7	4,5	0	0	11	1	0
B1-2	5	0,3	10	0,8	5	32	1	2
B1-3	8	1	12	0	5	17	2	2
B1-4	3	0,5	8	0	4	13	0	2
B1-5	4,5	0,5	12	0,5	4	9	8	2
B1-6	3	1	7	3	3	15	3	3
B1-7	4,5	1	6	0	3	19	1	2
B1-8	4,3	1	6	0	4	15	4	1
B2-1	2	0,3	5	0	2	24	2	1
B2-2	2	2	5	0	2	15	2	1
B2-3	5	2	4	0,3	4	14	5	0
B2-4	8,5	2	6	2	5	16	7	2
B2-5	3	0,5	7	0	5	48	10	3
B2-6	2,7	1,5	10	0	3	16	4	2
B2-7	9	2	10	0	3	21	3	1
B2-8	4	0,3	8	0	4	24	2	1
P-1	2,6	1	2	0,3	0	9	2	0
P-2	20	3	20	1	5	13	2	2
P-3	9,5	3	15	0	5	10	3	2
P-4	2,5	1	5	0,3	5	17	2	2
P-5	3,7	2	5	0	5	12	1	2
P-6	7	4	5	1	1	16	2	1
P-7	6	3	4	0	0	16	3	0
P-8	22	5	20	1	5	24	1	3

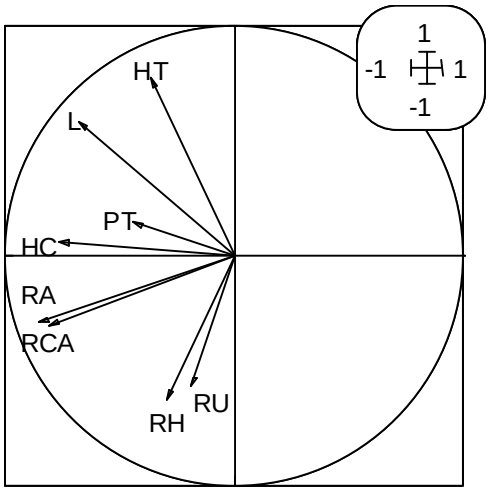
Ce tableau de données a été soumis à une analyse en composante principale (ACP) (l'axe 1 contient 35% de la variance et l'axe 2, 23%). Les résultats sont donnés figure A.9.

Il apparaît sur la projection que les haies des deux unités bocagères BOC1 et BOC2 sont très groupées et se démarquent des haies du site POL qui semble lui, beaucoup plus hétérogène car le nuage de points autour du barycentre est beaucoup plus éclaté que pour les deux autres sites. Sur l'axe 1, on trouve à une extrémité les stations P-2, P-3 et P-8 qui sont des haies de grande taille (largeur et hauteur) et richement boisées, à l'autre extrémité P-1 et P-7 (ainsi que B1-1) qui sont des haies peu larges, peu hautes et peu boisées et entre les deux toutes les haies des bocages qui ont un profil intermédiaire. L'axe F2 permet également de mettre en opposition les haies des polders qui ont une grande hauteur de talus aux haies des bocages, plus petites mais qui ont une richesse en herbacées et en arbustes plus importantes.

⇨ **Les paramètres de structure et de composition ne sont pas totalement dépendants de l'appartenance à un site : le gradient de l'axe F1 oppose des haies larges et très boisées à des haies étroites et peu boisées ; les stations des deux sites bocagers ont des profils assez proches alors que les stations des polders sont beaucoup plus hétérogènes. L'axe F2 oppose des haies riches en herbacées (BOC1 et BOC2) aux haies des polders qui ont une grande hauteur de talus.**



(a)



(b)

Figure A.9 (a) Projection des stations sur le plan factoriel F1-F2 représentant 58% de la variance (respectivement 35% et 23%) de l'ACP sur la matrice de structure et de composition des 24 stations. (b) Cercle de corrélation issu de l'ACP avec les variables de structure et de composition. Légende des variables : L = Largeur ; HT = Hauteur talus ; PF = Profondeur fossé ; HC = Hauteur moy. Canopée ; RCA = Recouvrement en arbres ; RH = Richesse en herbacées ; RU = Richesse en arbustes ; RA = Richesse en Arbres

2.2. Contexte paysager : occupation du sol et connectivité :

Afin de caractériser l'environnement entourant chaque station de piégeage, en terme d'occupation du sol et de connectivité, la première étape a été de choisir une taille de fenêtre adaptée et cohérente avec la perception du paysage du modèle biologique étudié, les petits mammifères. La taille de fenêtre a été choisie d'après la bibliographie et les données d'abondance des petits mammifères obtenues par le piégeage qui donnent le mulot largement dominant dans les communautés des trois sites (cf Chapitre 1) :

- 300 mètres autour de chaque station : car la distance instantanée moyenne parcourue par le mulot est de 300 à 500 mètres (Szacki and Liro 1991). Et une étude antérieure menée sur le site POL a montré qu'il y avait peu de différence d'occupation du sol entre des fenêtres de 200, 500 et 800 mètres (Paillat, 2000).

Pour valider ce choix, on a procédé à des mesures d'hétérogénéité dans des fenêtres de différentes tailles autour des stations de piégeage : 200m, 300m, 400m et 500m. L'hétérogénéité a été calculée a l'aide du logiciel Chloé, qui est un utilitaire d'analyse de structures spatiales basé sur le dénombrement des types de liaisons entre les grains d'une image (pixels), permettant ainsi le calcul d'un indice d'hétérogénéité selon la formule de Shannon (Shannon et Weiner, 1949). Le calcul de l'hétérogénéité est ainsi basé sur la formule suivante :

$$H = - \sum_{1}^{n} p(i,j).\log p(i,j)$$

i et j : couple de 2 pixels adjacents horizontalement et verticalement
p*(i,j)*.= fréquence du couple de pixels adjacents i et j
n = nombre de combinaisons existantes entre les couples de pixels

Les mesures des indices d'hétérogénéité (dans des rayons de 200, 300, 400 ou 500m) pour les 24 stations sont données en Annexe 5. A partir de ces valeurs, une matrice de corrélation de Pearson a été créée (Table A.5). Il apparaît que les mesures d'hétérogénéités à 200m, 300m, 400m et 500m sont toutes corrélées entre elles. On peut donc valider le choix d'une fenêtre à 300 mètres, qui est cohérent avec les caractéristiques de mouvement de l'espèce la plus mobile.

Table A.5 Matrice de corrélation de Pearson des valeurs d'indices d'hétérogénéité aux différentes tailles de fenêtres (en haut : le coefficient de corrélation de Pearson, en bas : la P-value associée).

	200m	300m	400m
300m	***0.905*** ***< 0.001***		
400m	***0.834*** ***< 0.001***	***0.955*** ***< 0.001***	
500m	***0.660*** ***< 0.001***	***0.850*** ***< 0.001***	***0.932*** ***< 0.001***

Des exemples de cartographie des fenêtres à 300 mètres sont données figure A.10 et laissent apparaître des différences nettes entre les stations de piégeage des trois sites. Le contour des fenêtres a été construit de manière à maintenir une distance constante de 300m à tous les points de la zone piégée, ce qui explique les formes différentes des fenêtres, directement influencées par les formes des haies.

A l'aide d'ArcView 8.3, les valeurs de surfaces relatives d'occupation du sol dans les fenêtres ont été extraites. Ont été considérées pour cette extraction les occupations du sol :

- Bois
- Prairie
- Maïs
- Céréales
- Légumes

Le bâti et les routes n'ont pas été pris en compte.

Une mesure de connectivité a aussi été extraite des cartes.

La connectivité est un concept fort de l'écologie du paysage, introduit par Meriam (1984), Baudry (1984), Forman et Gordon (1986), Baudry et Merriam (1988). Taylor et al. (1993) ont donné la définition suivante à la connectivité fonctionnelle : « *Landscape connectivity is the degree to which landscape facilitates or impedes movement among resources patch* ». Elle est fonction de la composition du paysage, de sa configuration (arrangement spatial des éléments du paysage), et de l'adaptation du comportement des organismes à ces deux variables (Burel et Baudry, 2001).

En pratique, de nombreuses mesures ont été utilisées pour rendre compte de la connectivité du paysage (Tischendorf et Fahrig, 2000). Souvent, elle se limite à la connectivité structurelle et est mesurée très simplement par une mesure de linéaire de haies (Apeldoorn et al, 1992 ; Paillat et Butet, 1996, 1997 ; Paillat, 2000). C'est cette méthode que nous avons choisi, en exprimant la connectivité par une densité du réseau de haies, en mètres par hectare de paysage pour la fenêtre considérée.

Les valeurs d'occupation du sol et de connectivité pour les fenêtres de 300m pour les 24 stations sont données Tableau A.6.

Tableau A.6 Occupation du sol et connectivité du réseau de haies dans des fenêtres de 300m autour des stations de piégeage.

	Fenêtre de 300 mètres					
	Bois (%)	Prai (%)	Mais (%)	Cere (%)	Legu (%)	Haie (m/ha)
B1-1	3,12	41,66	28,36	26,86	0,00	112,79
B1-2	21,64	64,41	11,17	2,79	0,00	85,56
B1-3	3,33	64,83	21,03	10,82	0,00	124,71
B1-4	6,82	50,89	22,99	19,29	0,00	113,19
B1-5	7,89	59,44	15,93	16,74	0,00	80,70
B1-6	13,49	49,93	18,32	17,51	0,75	123,77
B1-7	7,44	66,55	22,00	3,56	0,44	108,16
B1-8	4,73	52,51	21,60	21,16	0,00	130,43
B2-1	9,12	34,37	22,58	33,93	0,00	71,23
B2-2	1,09	11,60	56,36	30,94	0,00	25,08
B2-3	2,95	36,50	34,66	25,89	0,00	60,10
B2-4	0,00	23,43	27,26	49,30	0,00	39,81
B2-5	0,33	40,05	37,14	21,85	0,62	72,61
B2-6	0,34	40,51	36,30	22,52	0,34	56,57
B2-7	0,23	22,44	27,68	49,65	0,00	38,56
B2-8	13,23	48,20	26,47	8,36	3,73	66,01
P-1	0,00	14,61	25,55	27,41	32,43	28,90
P-2	0,00	0,00	33,40	25,97	40,62	27,98
P-3	0,00	42,39	10,10	17,79	29,72	12,66
P-4	0,00	29,20	26,00	5,72	39,07	28,98
P-5	0,00	20,05	16,01	16,50	47,44	17,42
P-6	0,00	7,51	32,68	11,29	48,51	8,16
P-7	0,00	7,74	27,33	15,67	49,26	20,00
P-8	1,85	3,98	36,49	14,46	43,22	34,39

Une analyse en composante principale a été effectuée sur les valeurs d'occupation du sol et de connectivité données dans la Tableau A.6 (Figure A.11).

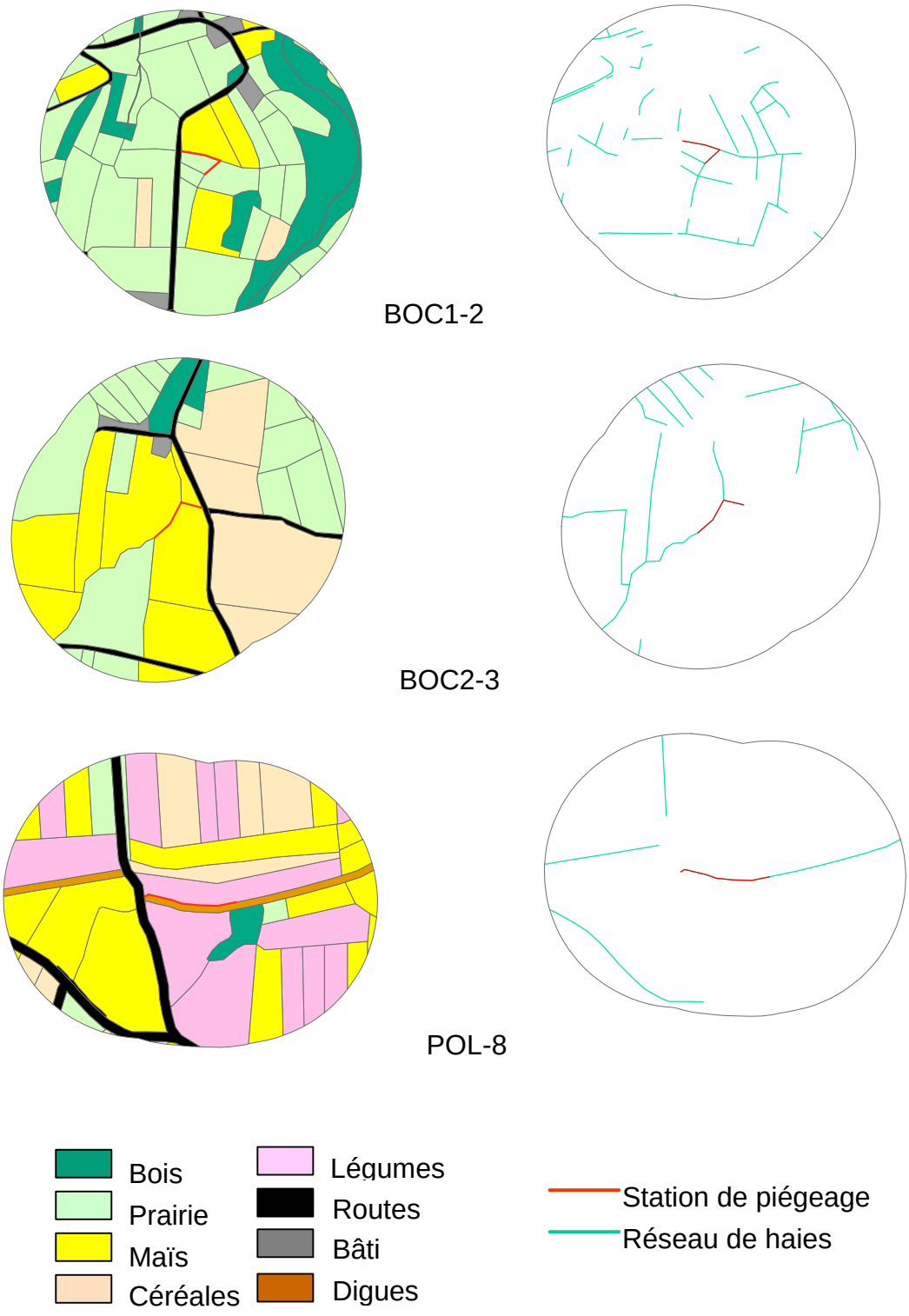


Figure A.10 Exemple de cartographie de l'occupation du sol et du réseau de haies dans un rayon de 300 mètres autour de trois haies de piégeage, BOC1-2, BOC2-3 et POL-8.

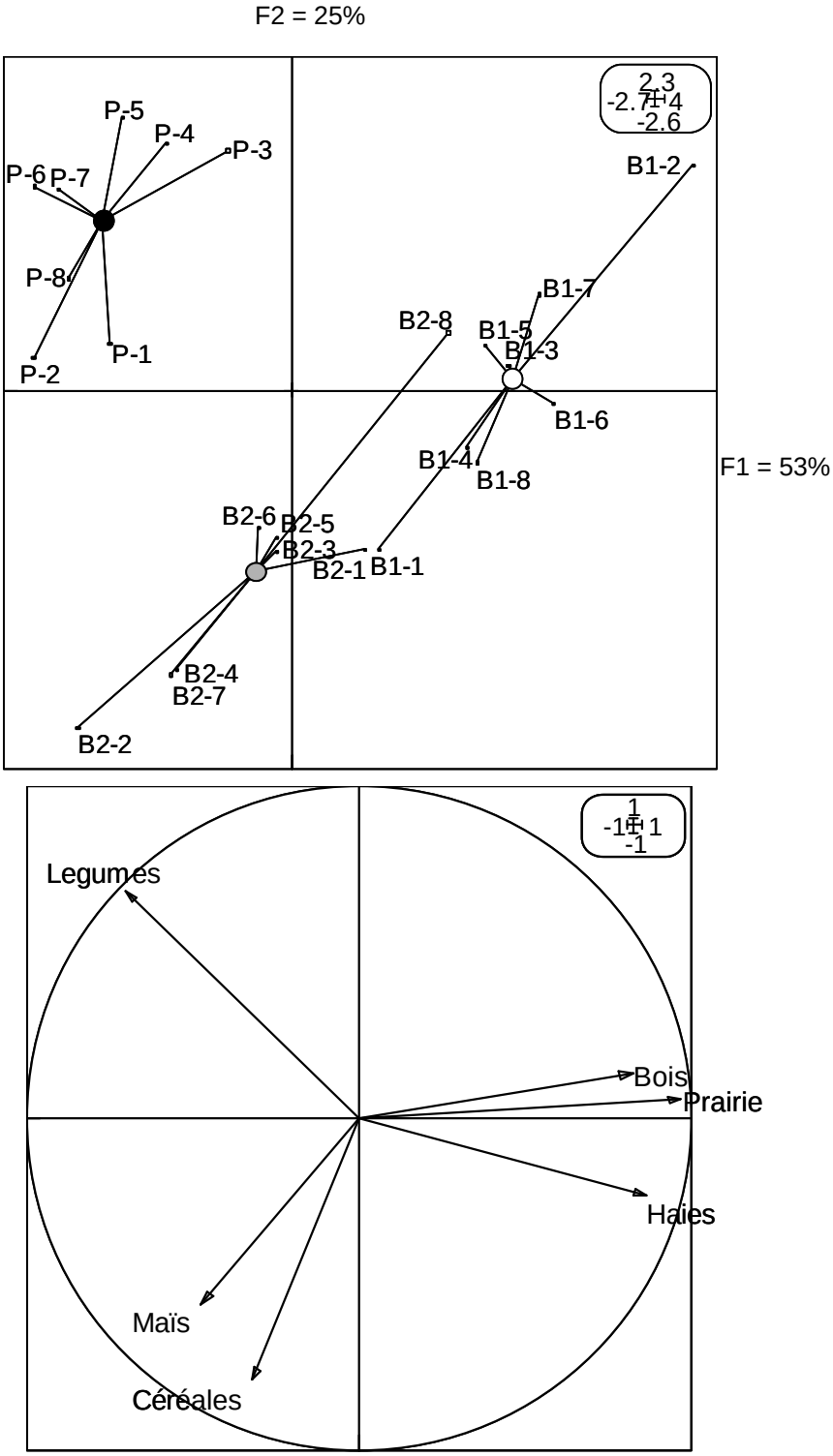


Figure A.11 (a) Projection des stations sur le plan factoriel F1-F2 représentant 61% de la variance (respectivement 53% et 25%) de l'ACP sur la matrice d'occupation du sol et de connectivité des 24 stations (les pourcentages d'occupation du sol sont transformés en ArcSinusRacine(x)). (b) Cercle de corrélation issu de l'ACP avec les variables d'occupation du sol et de connectivité.

L'analyse permet une bonne discrimination des stations selon leur environnement : trois groupes de haies sont clairement différenciées selon l'appartenance au site : les haies de POL sont toutes groupées ensemble, de même que les haies de BOC1 (à l'exception de BOC1-1, qui a un environnement plus proche des haies de BOC2) et pour les haies de BOC2 (à l'exception de BOC2-8 qui présente un environnement plus proche des haies de BOC1). L'axe F1 oppose d'un côté les haies de BOC1, fortement caractérisée par un environnement d'habitats permanents ou semi-permanents (prairies, bois et haies) et de l'autre côté les haies de POL avec peu d'habitats permanents à proximité mais beaucoup de cultures à rotation rapide (en particulier légumes). Les haies de BOC2 se situent en position intermédiaire. L'axe F2 tend à différencier les haies par le type de cultures environnant (légumes dans les polders versus céréales et maïs dans BOC2).

⇨

L'environnement agricole et la connectivité autour des 24 stations sont très liés à l'appartenance au site.
Comme ce qui avait été mis en évidence à l'échelle des sites entiers, les stations se situent sur un gradient d'ouverture du paysage (diminution de la densité de haies et de la proportion de bois) et d'intensification de l'usage des terres (diminution de la quantité de prairies au profit des cultures) : stations BOC1 < stations BOC2 < stations POL.
De plus, les haies de POL sont très entourées de légumes ce qui les oppose aux haies de BOC2, entourées par des céréales et du maïs.

CHAPITRE 1

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How does landscape use influence small mammal diversity, abundance and biomass in hedgerow networks of farming landscapes ?

Nadia MICHEL, Françoise BUREL and Alain BUTET

Accepté dans ACTA OECOLOGICA

Photographies aériennes des trois sites d'étude (BOC1, BOC2, POL). Source : IGN.

How does landscape use influence small mammal diversity, abundance and biomass in hedgerow networks of farming landscapes ?

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Runnig title : Small mammals in hedgerow networks of agricultural landscapes

Abstract

Over the last decades, profound changes in agricultural practices in the world have led to modifications of land-use as well as landscape structure and composition. Major changes resulted in enlargement of parcel size, increase of cultivated areas and drastic reduction of permanent elements such as woods, hedges or natural meadows.

In this context we chose to investigate the composition and structure of small mammal communities in the hedgerow networks of 3 landscape units of Western France (Brittany) differing by their level of agricultural land-use intensity and hedgerow network density : a slightly intensified dense hedgerow network landscape unit (BOC1), a moderately intensified and fragmented hedgerow network landscape unit (BOC2) and a highly intensified landscape unit on an area reclaimed from the sea (POL).

Characterization of small mammal communities was performed using live trapping on permanent habitats (8 hedges per landscape unit). In each of the 24 trapping units, a standardized method was used consisting of a baited 100m trap-line.

Diversity indices were used to compare the three communities. Species richness didn't vary across landscapes whereas Shannon's index of diversity underlined a clear difference between, on the one hand, the most intensified landscape unit (POL) which displayed the lowest diversity and, on the other hand, the two other less intensified units.

The abundance of small mammals differed between the three sites : they were significantly more numerous in the hedges of the most intensified site than in hedges of the two other sites. Differences between species also appeared: for example, the Bank vole (*Clethrionomys glareolus*) was very characteristic of POL, whereas the Pygmy shrew (*Sorex minutus*) was much more associated with BOC sites.

Within hedges, like for abundance, small mammal biomass was the highest in the most intensified site (POL > BOC2 = BOC1). On the contrary, at the landscape scale, biomass was the lowest in POL (BOC1 > BOC2 > POL) because of the fragmentation of the hedgerow network.

Key words

Biodiversity ; agricultural intensification ; farming landscapes ; small mammals community ; diversity ; biomass

Introduction

Rural landscapes have been used for agriculture and forestry for centuries (Bertrand, 1975). Today, arable farming is one of the most widespread forms of land use in the world (Stoate et al., 2001). Contrasting with natural landscapes, rural landscapes are controlled by human activities and ecological processes have a limited role in their evolution (Burel and Baudry, 1995). During the last decades, drastic changes in agricultural landscape structure and composition have been induced by changes in agricultural production methods, technological advances and government policies, affecting Europe (Burel and Baudry, 1990; Turner and Meyer, 1994; Robinson and Sutherland, 2002) and landscapes elsewhere in the world (Reardon et al., 1999; Allen and Ballard, 2001; Bourke, 2001; Bélanger and Grenier, 2002). The major modifications due to intensification of agriculture concern land use patterns with large increase of cultivated areas and fragmentation of uncultivated features such as forests (Hobbs and Saunders, 1993), natural meadows (Baudry, 1992) and hedgerows (Rackham, 1986). For example, in northern Brittany (western France) where agricultural landscapes are characterized by the presence of hedgerow networks, hedge length and connectivity fell by 22% and 35% respectively from 1952 to 1993 (Petit, 1994). This can be related to the enlargement of fields to facilitate the use of large machinery induced by modern arable management (Petit and Burel, 1998) and to reallotement policies. Moreover, the extensive use of pesticides and fertilizers, the increase of the disturbance regime and the simplification of cropping systems have also been major modifications of modern agriculture (McLaughlin and Mineau, 1995).

Impacts of these changes on biodiversity and ecological processes in agrosystems have received a great interest in numerous recent studies involving various taxas (Chamberlain and Fuller, 2000; Maisonneuve and Rioux, 2001; Robinson and Sutherland, 2002; Benton et al., 2003; Kleijn and Sutherland, 2003; Asteraki et al., 2004). The loss of ecological heterogeneity has contributed to the loss of suitable habitats for many species and resulted in significant implications for wild species of flora and fauna (Benton et al., 2003). For example, on a European scale, the change in cereal production accounts for 30% of the decline in farmland bird numbers (Donald et al., 2001); butterflies might be declining in northwest Europe because of the loss of unimproved pastures and changes in food-plant abundance (Smart et al.,

2004), and the management of hedgerows and field margins affects the abundance and diversity of flora (Boatman, 1984; de Snoo, 1999).

For several years, our landscape ecology research team has developed studies to understand how farming activities and landscape changes influence biodiversity (Burel et al., 2004). This paper investigates the composition and structure of small mammal communities of hedgerow networks in three landscapes units differing by their level of agricultural intensification.

Small mammals have received a great interest in numerous papers but not very often in this kind of biodiversity studies. They are generally considered as agricultural pests causing damage to agricultural products and are studied as such (Delattre et al., 1999 ; Hansson, 1989). Moreover, studies about small mammals are generally limited to the scale of the habitat (Geuse et al., 1985 ; Canova, 1992 ; Rychlik, 2000 ; Fox et al., 2003) and are not analysed at the scale of landscape gradients. Nevertheless, small mammals are in interesting biological model because they are ecologically important at the landscape scale: almost every terrestrial and avian carnivore, to some degree, depends on a small mammal prey base. For example, Love et al. (2000) detected food diet changes induced by agricultural intensification in a small mammal predator (*Tyto alba*, the Barn owl) .

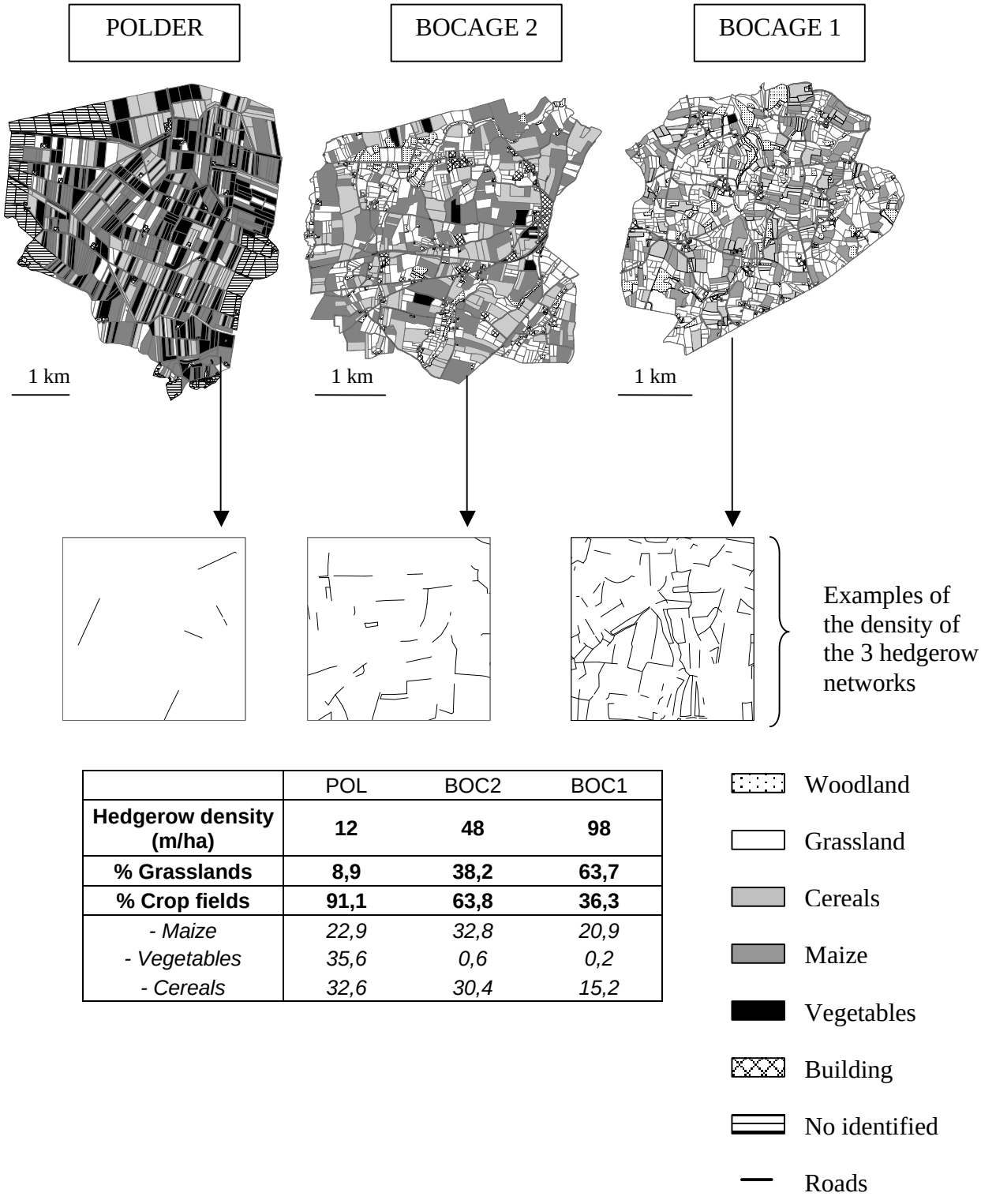
Our main goal was firstly to compare the small mammal communities living in the hedgerow networks of three contrasted landscapes, with respect to their species richness, diversity and abundance. As regards to previous works on the same sites (using Barn owl (*Tyto alba*) pellet analysis) (Paillat, 2000), and general knowledge on the relations between agriculture and biodiversity, richness, diversity and abundance were expected to be greater in the less modified landscapes. Another aspect of this work was to consider the communities as prey-communities determining prey availability for predators (determined from local to landscape scale).

Material and methods

1) Study site :

Our study area was situated in northern Brittany, south of the Mont Saint-Michel Bay (48° 36' N, 1° 32' W, western France). Three landscape units differing by their level of agricultural land-use intensity and hedgerow network density were chosen (Figure 1). A hedgerow network (locally named bocage) characterized two landscape units both oriented toward milk production : the first one (BOC1) was slightly intensified with a very dense hedgerow network, and the second one (BOC2) was moderately intensified and more open and fragmented because of land reallotment. The third unit (POL) was a highly intensified polder (on an area reclaimed from the sea) structured by a network of dykes with few hedges and intended for intensive cereal and vegetable production since 1970 (Le Grand, 1995). Areas of these landscape units are respectively 1019 ha for BOC1, 1659 ha for BOC2 and 2544 ha for POL. We essentially based the delimitation of the units on landscape structure drawn from aerial photographs. We took into account the grain size of the field mosaic, the density of hedgerow network, and the relative proportions of grassland vs. cropland. Hedgerow network densities were measured in the 3 sites using GIS (ArcView 8.2 software) : they were 98m/ha in BOC1, 48m/ha in BOC2 and 12m/ha in POL (Figure 1). Field surveys were carried out to determine land use in the three sites : 63.7%, 38.2% and 8.9% of grassland and 36.3%, 63.8% and 91.1% of crop fields for BOC1, BOC2 and POL respectively (Figure 1 for details).

In each site, eight hedges were chosen within the hedgerow network to be trapping units. They were selected far enough from one another to avoid spatial autocorrelation : the minimum distance between sampled hedges was 600m for BOC1 and 700m for BOC2 and POL.



	POL	BOC2	BOC1
Hedgerow density (m/ha)	**12**	**48**	**98**
% Grasslands	**8,9**	**38,2**	**63,7**
% Crop fields	**91,1**	**63,8**	**36,3**
- Maize	*22,9*	*32,8*	*20,9*
- Vegetables	*35,6*	*0,6*	*0,2*
- Cereals	*32,6*	*30,4*	*15,2*

Figure 1 : Soil occupation maps of the three landscape units (POL, BOC2, BOC1), examples of the hedgerow network densities in 1 km² windows and landscape characteristics.

2) Small mammal sampling method :

Each of the 24 trapping hedges was sampled seven times in April 2003, May 2003, June-July 2003, August 2003, September 2003, October 2003 and February 2004. Within each of the 7 trapping sessions, one week was necessary to sample all the 24 hedgerows (in random order) so we can consider that hedges were sampled simultaneously. We used a live-trapping method which is the most common method used to study small mammals (Gurnell and Flowerdew, 1990) and has been successfully used to detect patterns of richness, composition and abundance of small mammal communities across ecological gradients (Patterson et al., 1989 ; Yu, 1996 ; Kelt, 1996). We used a standardized method (Spitz et al., 1974) consisting of a 100 m line of 34 baited (wheat flour and margarine mixture and a piece of apple) live-traps spaced every 3 m. Two visits were made at dawn, 24 hours and 48 hours after installation. Individuals captured on the first visit were temporarily marked (colour mark on the tail) to avoid considering them twice if recaptured on the second visit.

We used INRA live traps (a French live-trap model) that are very efficient in catching both shrews and rodents (Aubry, 1950), even it is known that live-trapping techniques may induce biases in relative abundance estimates of species (Sullivan et al., 2003). According to the objectives of our study, comparisons of small mammal abundance between landscapes were more important than inter-species comparisons in a particular landscape. Finally we consider our trapping procedure to be efficient in furnishing reliable comparative estimates of relative abundance of small mammals in the three different examined landscapes.

The total number of individuals trapped (excluding recaptures) was used as an index of abundance of each species (Hansson, 1967). Every individual caught was weighed to the nearest 0.5 g. The mean relative local biomass (g/100 m) of animals caught was calculated by summing the weight of all individuals captured within each hedge and by averaging the obtained value in the eight hedges within each site. We then estimated the landscape relative biomass (g/ha) by weighting this mean local biomass with the hedgerow densities of the three sites.

3) Data analysis :

Species richness (S), Shannon-Weaver index of diversity (H') and equitability (=evenness) (J=H/lnS) were used to compare small mammals assemblages between the three sites (Shannon and Weiner, 1949 ; Magurran 1988 ; Silva, 2001). Such indices are often used to characterise biodiversity (Canova and Fasola, 1991 ; Bryja and Rehak, 1998), particularly in comparative studies and we hypothesize that they should reflect the response of small mammal assemblages to changes in landscape structure. Shannon's diversity indices were compared between sites using Hutcheson's test (Hutcheson 1970 ; Lande, 1996).

Multivariate analysis was performed using ADE-4 software^{TM} (Thioulouse et al. 1997). Possible effect of site on species abundance in sampled hedges was checked using one-way ANOVA. A discriminant between-group analysis was performed on the table of abundance of the eight species in the 24 sampling units. Projections of species and sampling units were performed on the first factorial plane of the analysis.

The Student T-test was used to compare the average relative biomass of the communities in the three sites.

Results

During a 11,424 trap-nights effort, a total of 1379 catches were obtained in this study of which 1191 (86%) were rodents and 188 (14%) were shrews. Eight species were captured during the whole year of trapping. Four rodents species were found: *Apodemus sylvaticus*, As (Wood mouse) (Linné 1758), *Clethrionomys glareolus*, Cg (Bank vole) (Schreber 1780), *Microtus agrestis*, Mag (Field vole) (Linné 1761), *Microtus subterraneus*, Ms (Common pine vole) (de Sélys-Longchamps 1836) and four insectivores species: *Crocidura russula*, Cr (White-toothed shrew) (Hermann 1780), *Neomys fodiens*, Nf (Aquatic shrew) (Pennant 1771), *Sorex coronatus*, Sc (Common shrew) (Millet 1828), *Sorex minutus*, Sm (Pigmy shrew) (Linné 1766). Total abundance of each species in each site is given in Table 1.1.

Table 1.1 : Data of species captures in the three sites.
Total catches per site (T), species richness (S), Shannon's diversity (H') and equitability (J) of the small mammal communities in the three sites are given.
** Significance difference between diversity using Hutcheson's test ($p<0.01$).

	BOC1	BOC2	POL
SPECIES			
Wood mouse *Apodemus sylvaticus*	249	228	386
Bank vole *Clethrionomys glareolus*	37	58	177
Field vole *Microtus agrestis*	8	5	1
Common pine vole *Microtus subterraneus*	19	8	15
White-toothed shrew *Crocidura russula*	18	35	20
Aquatic shrew *Neomys fodiens*	1	2	0
Common shrew *Sorex coronatus*	25	38	16
Pygmy shrew *Sorex minutus*	16	15	2
INDICES			
T	373	389	617
S	8	8	7
H'	1.75	1.92	1.41**
J	0.58	0.64	0.50

Total abundance of small mammals differed between the three sites : captures being about 1.6 times greater in POL than in BOC1 and BOC2 (Table I). The same eight species were found in BOC1 and BOC2 and only seven species in POL (Table I). This difference in species richness was due to the absence of the water shrew, *Neomys fodiens* in POL (Table 1.1). Shannon's diversity index (H') in BOC1 (1.75) and in BOC2 (1.92) were significantly higher than in POL ($p<0.01$) (Table I). Equitability (J) was also the lowest in POL (Table 1.1), which may be attributed to the predominance of the wood mouse, *A. sylvaticus*, and the bank vole, *C. glareolus*, in the polder.

The wood mouse was the dominant species across all sites, representing 67% of the total numbers in BOC1, 59% in BOC2 and 63% in POL. The bank vole, was also well represented, particularly in POL with 29% of the total numbers, this proportion being of only 10% and 15% in BOC1 and BOC2. The six other species were much scarcer, always showing a relative abundance lower than 10%.

The between-group test performed on total numbers in each sampling hedge (log-transformed data) shows a significant inter-site inertia ($p<0.007$) indicating that the pattern of captures in the three sites are different.

To identify which species influence this result, a one-way ANOVA was performed (Table 1.2). Abundances of *Clethrionomys glareolus* and *Sorex minutus* responded significantly to the site factor ($p<0.05$) whereas *Apodemus sylvaticus, Microtus subterraneus, Crocidura russula, Neomys fodiens* and *Sorex coronatus* were not significantly influenced by site factor.

Table II :
Effect of site on the total abundance of small mammals in sampled hedges
(Oneway ANOVA)
*** = F highly significant (p<0.01)
** = F highly significant (p<0.05)
ns = non significant

Species	*Source*	*SS*	*d.f.*	*MS*	*F*	*P-value*	*Significance*
As	Between	0.2393	2	0.1196	2.698	0.0891	ns
	Within	0.9312	21	0.0443			
	Total	1.171	23				
Cg	Between	1.629	2	0.8143	4.488	0.0235	**
	Within	3.81	21	0.1814			
	Total	5.439	23				
Mag	Between	0.1814	2	0.0907	2.677	0.0906	ns
	Within	0.7115	21	0.0339			
	Total	0.8929	23				
Ms	Between	0.0583	2	0.0291	0.2337	0.796	ns
	Within	2.619	21	0.1247			
	Total	2.677	23				
Cr	Between	0.174	2	0.0870	0.627	0.5485	ns
	Within	2.913	21	0.1387			
	Total	3.087	23				
Nf	Between	0.0145	2	0.0083	0.5487	0.5907	ns
	Within	0.2785	21	0.0133			
	Total	0.293	23				
Sc	Between	0.4404	2	0.2202	2.804	0.0819	ns
	Within	1.649	21	0.0785			
	Total	2.09	23				
Sm	Between	0.6107	2	0.3054	6.874	0.0051	***
	Within	0.9328	21	0.444			
	Total	1.544	23				

The first factorial axis (PC1) of the between-group analysis accounted for 92% of the total inertia so we made the interpretation of the analysis only on this axis (Figure 1.2A). In the factorial map of sampled hedges derived from the between-group analysis, the first factorial plane shows a clear opposition between on the one hand BOC1 and BOC2 whose centres of gravity are very close, and on the other hand, POL (Figure 1.2A). Absolute contributions of the eight species to the first axis are given in Figure 2C. *S. minutus* and *C. glareolus* presented the highest contributions; *A. sylvaticus*, *S. coronatus* and *M. agrestis* also had high contributions and finally *M. subterraneus, C. russula* and *N. fodiens* almost didn't contribute to the inertia of the axis. The bank vole (Cg) and the wood mouse (As) seemed to be particularly associated with the POL site whereas shrews and other voles were more characteristics of the BOC sites (Figure 1.2B).

Relative local average biomass in sampled hedges (grams of small mammals per 100m trap-line) was quite similar for BOC1 and BOC2 whereas it was significantly higher in POL ($p<0.05$) (Figure 1.3A). This could be due to the average width of the sampled hedges which is double in POL (respectively 4.3, 4.5 and 9.1 m for BOC1, BOC2 and POL). In contrast to the local values obtained in individual hedges, landscape biomass was the highest in BOC1, intermediate in BOC2 and the lowest in POL (Figure 1.3B).

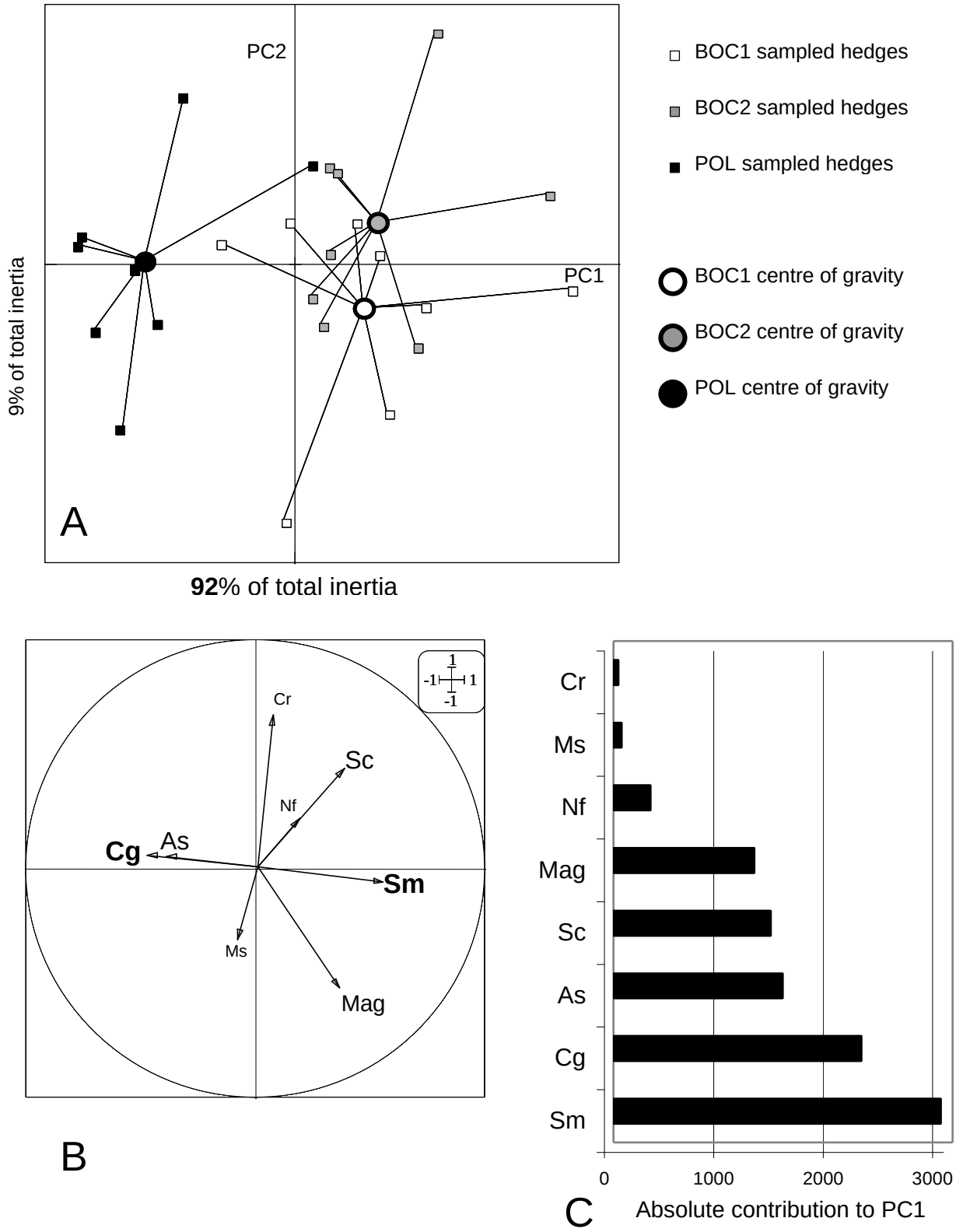
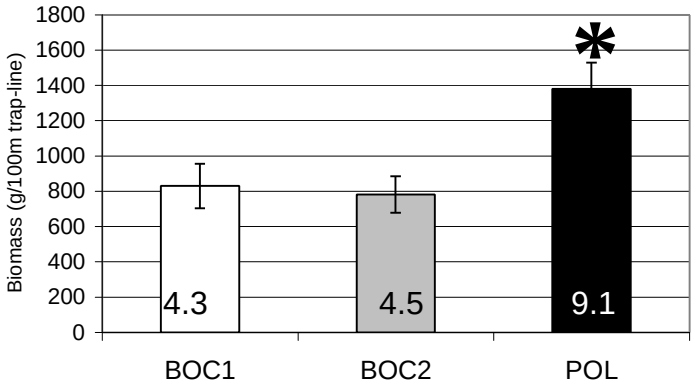


Figure 1.2 : Graphical interpretation of the between-groups analysis computed on total species abundance in each sampled hedge (log-transformed data).
A : sampled hedges projection on the first factorial plane F1-F2. The centre of gravity of each site (circles) is linked to its corresponding samples. Inertia explained by the factorial axes is provided.
B : correlation circle indicating species.
C : absolute contributions of species to the first factorial axis.

A



B

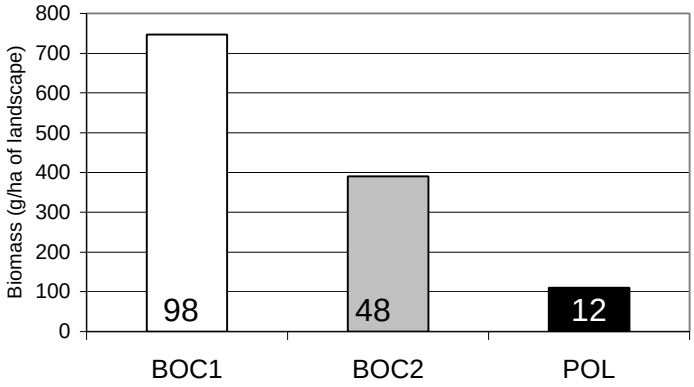


Figure 1.3 :
A : Relative local average biomass of the small mammals communities in the sampled hedgerows of the 3 sites (g/100 m of trap-line) with the values of the average width of the sampled hedges (meters).
* Significance difference between biomass using Student t-test ($p<0.05$).
B : Relative weighted (by the landscape hedgerow densities) landscape biomass of the small mammals in the hedgerow network of the 3 sites (g/ha of landscape) with the values of the hedgerow network densities (m/ha).

Discussion

1) Diversity indices :

In our study, agricultural intensification did not have a significant influence on the species richness of the small mammal communities. Similar results derived from barn owl pellet analysis were obtained in the same sites by Paillat (2000) and by Millan de la Pena et al. (2003) on a 11 sites gradient of agricultural intensification. Robinson and Sutherland (2002) also assumed that agricultural intensification in Great Britain only had led to a decrease in abundance and maintained species richness of small mammals. Other studies on different taxa also show no effect of agri-environmental schemes on species richness : Feehan et al. (2002) for carabids and plants and Flynn et al. (2002) for birds.

In fact, in our study, 7 of the 8 species were common to the three sites whereas only one (the water shrew) was absent in the more intensified landscape, but we captured only one individual in BOC1 and two individuals in BOC2, which did not represent a significant difference. It is interesting to note that this rare species, the water shrew, *Neomys fodiens*, is protected by law in France (Fiers. et al., 1997). Intensification of agriculture appears to be a threat for the conservation of the water shrew which seems to be sensitive to disturbance and to show a better survival in landscapes providing sufficient areas of uncultivated stable habitats (Millan de la Pena, 2003) such as dense bush and high vegetation of “humid zone” (Paillat and Butet, 1997). For the 7 other species which were common to the three sites, local rarity could occur at the scale of one sampled hedge but not at the landscape scale, as shown by Merriam and Wegner (1992). In the case of strictly habitat dependent species, such as the bank vole, local extinction could occur in small or isolated habitats (Paillat and Butet, 1996 ; Van Apeldoorn et al., 1992) but species could however easily colonize vacant territories. For these reasons, species richness seemed not to be a good indicator to characterize the effect of agricultural intensification on small mammal communities which is in agreement with previous findings in those sites (Burel et al., 1998 ; Milla de la Pena et al., 2003).

On the other hand, Shannon's diversity and equitability indices underlined a clear contrast between the three sites, showing a major difference between the more intensified site (POL) on the one hand, which displayed the lowest diversity and evenness, and the two other landscapes, slightly (BOC1) and moderately (BOC2) intensified. Generally, agricultural intensification leads to a loss of diversity (Robinson and Sutherland 2002) with the increase of common and generalist species (i.e. the Wood mouse, Love et al., 2000) to the detriment of specialist and scarce species (Kleijn and Sutherland 2003). Studies showed that butterfly species that occur widely in farmland generally didn't decline with agricultural intensification whereas those with restricted habitats (i.e. grassland) decreased (Pollard et al., 1995 ; Asher et al., 2001). A number of field studies across Europe also showed declines in many carabid species, with a few species becoming more common and dominating the assemblage (Luff and Woiwod, 1995 ; Kromp, 1999).

2) Abundance :

The two sites of "bocage", BOC1 and BOC2 showed a similar total number of captures which were lower than in the most intensified site.

This is also clearly shown by the between-groups analysis which identifies the Bank vole, the Wood mouse, and the Pygmy shrew as major species influencing this contrast. The fact that the wood mouse is well represented in the most intensified site could be explained by its high dispersal capacity which could be independent of the hedgerow networks (Geuse et al., 1985 ; Wolton, 1985) and by the fact that it certainly benefits from landscape heterogeneity to find and exploit food resources. For example, cereal crops provide greater availability of seeds and can improve population densities of the wood mouse, a typical seed-eater. This species has a large ecological niche and is not sensitive to the habitat transformations. It is generally considered as opportunistic and able to rapidly colonize good resource patches or newly created habitats in heterogeneous landscapes (Halle, 1993). It can move across a large range of patches as a function of the resource availability (Tew et al., 1992), and can exploit both cultivated fields and hedge habitats (Pollard and Relton, 1970 ; Kikkawa, 1964).

It was more surprising that Bank voles were so abundant in the most intensified site because this species is known to have a low mobility (Bauchau and Le Boulengé, 1991), to be

very sensitive to habitat fragmentation (Van Apeldoorn, 1992 ; Paillat and Butet, 1996) and to be restricted to hedges, not moving far into adjoining fields, and is probably dependent on woody or other dense cover for its existence in farmland (Pollard and Relton, 1970). Its predominance in the Polder site could be due a larger width of hedges in POL compared with Bocage sites, reducing the edge effect (Canova et al., 1991), and thus enhancing habitat quality for specialists such as the bank vole (Tattersall et al. 2002).

On the other hand, it is easier to understand why the Pygmy shrew is more abundant in the less intensified sites. This species is known to be very dependent on moist habitats (swamps, humid woodlands, wet meadows, reed beds) and/or densely wooded landscapes (Lovari et al., 1976 ; Böhme, 1978 ; Taberlet, 1986 ; Spitzenberger, 1990 ; Hutterer, 1990). It is obvious that highly intensified landscapes contain a lower proportion of such residual natural habitats (Millan de la Pena et al., 2003). Thus, the Pygmy shrew seems to be a good indicator of hedgerow network fragmentation and of the evolution of land-use.

Data on the composition of small mammal communities in agricultural landscapes have mostly been derived from Barn owl pellet analysis. Love et al. (2000) compared the results of a 1993-1997 study with those of a similar one covering the period 1956-1974, permitting to underline the effects of agricultural intensification on the community. Between these two periods, the Barn owl (*Tyto alba*) diet had changed significantly, showing an increase of the proportion of *Apodemus* and *Clethrionomys glareolus*, which is consistent with our results. However, they also found an increase in the Pygmy shrews (*Sorex minutus)* contrarily to what would be expected from our study which shows that agricultural intensification decreases the abundance of this species. It should be interesting to know if such conflicting results for this species are the fact of a bias induced by the use of two different methods (direct trapping versus indirect barn owl pellet analysis). In the case of our study sites, both methods show similar trends in the community, with a clear opposition between the Polder site and the Bocage sites (see Paillat (2000) for barn owl pellet analysis results).

3) Biomass :

It was unexpected to note that, at a local scale, the hedges of the Polder site, despite the stronger level of agricultural intensification present the highest small mammal biomass. In

scarce literature available about small mammal communities viewed as prey resources available to predators, there are no such examples (similar or contrary). Nevertheless, the greater width of those Polder hedges may lead to a greater trophic availability (Schoener, 1983) for small mammals, and could permit to host a larger number of animals, resulting in a greater biomass. Habitat structure and composition probably determine the quality and abundance of food (Dueser and Shugart 1979) and might influence community structure (Canova and Fasola, 1991). Large hedges could also constitute better anti-predation shelters by reducing the edge effect : a lowered predation pressure could consequently enhance the quantity of small mammals. Moreover, even if the landscape gradient is linked to the hedgerow network density, it is possible that intrinsic characteristics of the polder hedges may be different from the bocage hedges because of contrasting origins.

At the landscape scale, there is a decreasing gradient of prey-resource biomass (BOC1 > BOC2 > POL) with increasing agricultural intensification. It would be interesting to study the effects of those varying prey availability on predators (running survey). In fact, landscape composition and structure determines both diversity of predator communities and the variations in prey-resource abundance (Raoul et al., 2001). Any change in prey availability may have serious consequences for Barn owls and other small mammal predators (Massemin and Handrich, 1997). Moreover, Leptich (1994) showed a decreased abundance and diversity of raptors in areas highly developed for agriculture, and in the same study sites, Kessler (1979) found that the relative abundance of small mammals on slightly intensified area was greater than on highly developed area. Also, lowered prey densities in agricultural areas were responsible for differences in raptor nesting densities (Howard et al., 1976 ; Howard and Sather-Blair, 1983). Nevertheless, in our study, prey availability was only estimated in hedgerows, and it should be necessary to sample other habitats, such as grasslands, to obtain a more reliable estimation of landscape biomass for linking it to raptor abundances.

Conclusion :

Agricultural intensification on our three study sites (i.e. hedgerow network fragmentation and decrease, crop increase) seems to make the small mammal community less diverse but locally more abundant, leading to a greater local biomass availability in hedges. It remains difficult to understand if greater small mammal abundance and biomass in the hedges

of the most intensified landscape unit reflects differences in landscape context, habitat quality (linked to the history of the landscape) or predator pressure. Nevertheless, at the level of the landscape units, the highest density of the hedgerow network permits to host the highest prey biomass for predators. Moreover, within-site variability also appears and further investigations should be required to determine which factors could explain local community characteristics in hedges (i.e. structure, composition and quality of hedges, landscape context). Future investigations should also be carried out to understand how these differences influence the structure and composition of predator communities.

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CHAPITRE 2

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Role of habitat and landscape in structuring small mammal assemblages in hedgerow networks of contrasted farming landscapes in Brittany, France

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Soumis à LANDSCAPE ECOLOGY

Clethrionomys glareolus

Apodemus sylvaticus

Une haie du bocage (site BOC2) (Photo : Yann Rantier, 2005)

Role of habitat and landscape in structuring small mammal assemblages in hedgerow networks of contrasted farming landscapes in Brittany, France

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Running title : Habitat and landscape influence small mammal assemblages in hedgerows

Abstract

In this study, we investigated the environmental factors driving small mammal (rodents and shrews) assemblages in permanent habitat patches in response to a gradient of agricultural intensification. Small mammals were sampled using a trapping standard method in the hedgerow networks of three contrasted landscapes differing by their level of land-use intensity and hedgerow network density (BOC1: slightly intensified; BOC2: moderately intensified and POL: highly intensified). We hypothesized that both habitat and landscape characteristics have to be considered to understand the structure of local community at the level of habitat patches. In that way, we carried out a multi-scale study using environmental variables ranging from local habitat (structure and composition of the hedgerows) to hedgerows neighbourhoods in a radius of 300 m (land cover and connectivity around hedges) and to landscape units (three sites). During one year, 24 hedgerows were sampled seven times, representing a total of 1379 captures (86% of rodents and 14% of shrews) and eight species, dominated by the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*). Inter-site variability was significant and accounted for 18% of total variation in small mammal species abundances. But intra-site variability was also highlighted: species abundance profiles may differ greatly among hedgerows within a site. The more explanatory variables were identified at the different scales of the study: the landscape unit POL was shown to be an important factor in structuring the community, but the predominant factors explaining differences of abundances among hedgerows were about local habitat. In fact, the width of hedges and the tree species richness appeared to be significant and explaining the greatest part of the total variation of the small mammal community composition.

Keywords

biodiversity; small mammals; community; agricultural intensification; farming landscapes; habitat; multi-scale;

Introduction

Farmland represents the major land use in Europe and France (Fitzgibbon 1997). The total area of cultivated land increased by 466% in the world from 1700 to 1980 (Meyer and Tuner II 1992). While ancient agricultural systems had favourable for biodiversity in Europe over the centuries (Piorr 2003), the intensification of agricultural practices in the 20th century have led to a significant loss of natural and semi-natural elements of farming landscapes, inducing negative impacts on many of their floral and faunal components (Duelli and Obrist 2003).

The most important changes in agriculture have occurred since the 1950's (Burel and Baudry 1995; Turner and Meyer 1994; Robinson and Sutherland 2002). They concern: the increase of machinery use, and the introduction of new crops, agricultural practices and farming systems (Canévet 1992; Robinson and Sutherland 2002), the expansion of parcel size associated with fragmentation and loss of semi-natural elements such as woodlots, hedgerows or meadows (Leonard et Cobham 1997; Agger et Brandt 1988; Meeus 1990), the increase of cultivated areas and finally the growing use of chemicals such as fertilizers and pesticides (McLaughlin and Mineau 1995; Stoate et al. 2001). Such changes have occurred in Brittany, Western France, associated with land-use intensification (increase in production per surface unit) and reallotment policies.

These changes have influenced the dynamics of biodiversity in agricultural landscapes (McLaughlin and Mineau 1995): the loss of ecological heterogeneity in agricultural landscapes induced by modern arable management has contributed to the loss of suitable habitats for many species (Legendre 1993; Wiens et al. 1993) and resulted in significant implications for farmland species of flora and fauna.

Within such a context, and with the emergence of landscape ecology, growing scientific attention has focused on the conservation and study of the different types of farmland semi-natural habitats constituting the rural landscape mosaic (Freemark et al. 2002), with a central place taken by hedgerows (Baudry et al. 2000). In fact, beside the aesthetical aspects and protection against wind and erosion, hedgerows and hedgerow networks form an

essential part of rural biodiversity, carrying a broad range of different faunal and floral species (Hinsley and Bellamy 2000; Tattersall et al. 2002).

Small mammals (rodents and shrews < 40 g) are a common feature of agricultural landscapes and most farming practices cause stress to them by removal of shelter, food, as well as breeding and overwintering sites (Tew and Macdonald 1993). For several small mammals, hedgerows serve as permanent habitats (even if a use of adjacent crop fields is possible for certain species when cover is available and sufficient) (Burel 1996). Small mammals have a major role in ecosystems due to their function as prey: they provide an important food source for predatory mammals and birds (King 1985), some of which are becoming rare (e.g. *Tyto alba* in the British Isles (Fitzgibbon 1997)). With their high energy requirements and voracious feedings habits, shrews are an important component of the dynamics of terrestrial ecosystems (Churchfield et al. 2004). Rodents may also be important in promoting tree regeneration in woodland and along hedges (Hayward and Phillipson 1979). But they are still regarded as major pests in agriculture causing crop damages, which have motivated numerous studies (Batzli and Pitelka 1971; Giraudoux et al. 1994). Several studies have also examined the effects of farming practices on population dynamics and demography (Jacob 2002).

Previous studies have been carried out in Brittany to link small mammal assemblages to landscape or local habitat characteristics in farming landscapes: Millan de la Pena et al. (2003) studied the relationship between the small mammal community and landscape descriptors, using Barn owl (*Tyto alba*) pellet analysis in different sites. They showed that variations in species frequency could be observed in response to agricultural intensification and that the prevalence of some species allowed to distinguish different assemblages, which were characteristics of low, medium or high intensified landscapes, as confirmed by Michel et al. (in press). Paillat (2000) and Butet et al. (in press) investigated the local factors driving diversity and abundance of small mammal species inhabiting permanent habitat patches in an intensive agricultural landscape; they showed a clear difference among communities from grassy field boundaries and hedgerows. But those two studies were restricted to one scale, a gradient of landscape units in Millan de la Pena et al. (2003), and local habitat patches within a single landscape unit in Paillat (2000) and Butet et al. (in press). In the present study, we wanted to integrate both scales, by comparing species abundances of the small mammal community in hedgerows belonging to three landscape units differing by their level of agricultural intensity. The main goal was to identify environmental variables that could

explain the observed differences in species assemblages abundances among the hedges. As it is known that both landscape (Hansson 1977; Barrett and Peles 1999) and habitat (Bowman et al. 2001) can influence composition of small mammal assemblages, we carried out a multi-scale study using environmental variables ranging from local habitat (structure and composition of the hedgerows) to hedgerows neighbourhoods (land cover and connectivity around hedges) and to landscape units (three sites).

Material and methods

1) Study area and trapping sites :

The study took place in Brittany (department of Ille-et-Vilaine), south of the Mont Saint-Michel Bay (48° 36' N, 1° 32' W, North-Western France). Three landscape units were chosen in a study area named "Site Atelier de Pleine-Fougères" were several studies have been conducted on different biological models (Burel et al. 2004) in response to agricultural intensification. We essentially based the delimitation of the units on landscape structure drawn from aerial photographs. We took into account the grain size of the field mosaic, the density of hedgerow network, and the relative abundance of grassland vs. cropland. The three chosen sites are known to form a gradient of agricultural land-use intensity and hedgerow network density (Table 2.1). The first landscape unit (BOC1) is locally called "bocage" (common in Brittany, characterized by a dense hedgerow network). In BOC1, farming systems are exclusively oriented toward dairy production; 2/3 of the UAA (Used Agricultural Area) is covered by grasslands and fodder crops and milk cows predominate in the livestock. The second site, called BOC2, is also a "bocage", but the hedgerow network density is reduced. BOC2 is more intensified than BOC1: agriculture is mainly oriented toward mixed dairy-cattle and some crop production, with 1/3 of the UAA covered by grasslands and fodder crops. Finally, the third landscape unit, called POL, is a polder, reclaimed from the sea area with a network of dykes with few hedgerows. It is highly intensified with 90% of the UAA being crop fields; agriculture is oriented toward cereals and vegetables production. The landscape unit areas are respectively 1019 ha for BOC1, 1659 ha for BOC2, and 2544 ha for POL.

In each site, 8 hedgerows were chosen among the network to become the sampling units for trapping small mammals. They were chosen to be as distant as possible from one another, with 600 m minimum distance between hedges in BOC1 and 700 m in BOC2 and POL.

Table 2.1
Characteristics of the three landscape units : structure (mean parcel size and connectivity) and composition (proportion of the land covered by grasslands and crop fields, corn, vegetables and cereals).

	Landscape unit		
	BOC1	**BOC2**	**POL**
Mean parcel size (ha)	0.65	1.08	2.54
Connectivity			
Wood density (m²/ha)	803	424	13
Hedgerow density (m/ha)	98	48	12
Land-cover			
% Grasslands	**63.7**	**38.2**	**8.9**
% Crop fields	**36.3**	**63.8**	**91.1**
- % Corn	*20.9*	*32,8*	*22.9*
- % Vegetables	*0,2*	*0.6*	*35,6*
- % Cereals	*15.2*	*30.4*	*32.6*

In order to characterize the hedgerows, we extracted environmental variables at three scales (Table 2.2):

1. The first scale is the local habitat. We measured local variables of structure and composition. For physical structure: width of the hedges (m), average height of the canopy (m), and cover of the tree layer (index from 0 to 5). For vegetation composition, we made an extensive survey of the plant species present in the three layers (herbaceous, shrub and tree layer) of each sampled hedgerow. We then calculated herbaceous, shrub, and tree species richness indices.

2. The second scale was a land-cover neighbourhood window around each sampled hedge. The size of the window was chosen to be 300 m, which corresponds to the capacity of instantaneous movement of the most abundant species in the small mammal community, the wood mouse (*Apodemus sylvaticus*) (Szacki and Liro 1991). We used a Geographic Information System to determine the percentage of vegetables, corn, cereals, grasslands and woods, and the density of hedgerows in the 300 m windows.

3. The third scale is the landscape unit scale. The variables (binary) are consequently BOC1, BOC2 and POL.

Table 2.2
Characterization of the 24 sampled hedgerows at three scale, local habitat structure and composition, land-cover in a 300m window and landscape unit.
W=width (meters), ACH=average height of canopy (meters), CTL=cover tree layer (from 0 to 5 : 0=0%, 1=1-10%, 2=10-25%, 3=25-50%, 4=50-75%, 5= >75%).
HR=herbaceous species richness, SR=shrub species richness and TR=tree species richness.
wood=% of wood, grass=% of grassland, corn=% of corn, cere=% of cereals, veg=% of vegetables and hedge=hedgerow network density in the 300m window around each hedge.

Scale	Local habitat						300 m window						Landscape
	Structure			Composition									
Hedges	W	ACH	CTL	HR	SR	TR	wood (%)	grass (%)	corn (%)	cere (%)	veg (%)	hedge (m/ha)	Unit
B1-1	2.3	5	0	11	1	0	3.12	41.66	28.36	26.86	0.00	112.79	BOC1
B1-2	5	17	5	32	1	2	21.64	64.41	11.17	2.79	0.00	85.56	
B1-3	8	16	5	17	2	2	3.33	64.83	21.03	10.82	0.00	124.71	
B1-4	3	15	4	13	0	2	6.82	50.89	22.99	19.29	0.00	113.19	
B1-5	4.5	20	4	9	8	2	7.89	59.44	15.93	16.74	0.00	80.70	
B1-6	3	18	3	15	3	3	13.49	49.93	18.32	17.51	0.75	123.77	
B1-7	4.5	15	3	19	1	2	7.44	66.55	22.00	3.56	0.44	108.16	
B1-8	4.3	15	4	15	4	1	4.73	52.51	21.60	21.16	0.00	130.43	
B2-1	2	15	2	24	2	1	9.12	34.37	22.58	33.93	0.00	71.23	BOC2
B2-2	2	12	2	15	2	1	1.09	11.60	56.36	30.94	0.00	25.08	
B2-3	5	8	4	14	5	0	2.95	36.50	34.66	25.89	0.00	60.10	
B2-4	8.5	12	5	16	7	2	0.00	23.43	27.26	49.30	0.00	39.81	
B2-5	3	12	5	48	10	3	0.33	40.05	37.14	21.85	0.62	72.61	
B2-6	2.7	12	3	16	4	2	0.34	40.51	36.30	22.52	0.34	56.57	
B2-7	9	5	3	21	3	1	0.23	22.44	27.68	49.65	0.00	38.56	
B2-8	4	20	4	24	2	1	13.23	48.20	26.47	8.36	3.73	66.01	
P-1	2.6	5	0	9	2	0	0.00	14.61	25.55	27.41	32.43	28.90	POL
P-2	20	20	5	13	2	2	0.00	0.00	33.40	25.97	40.62	27.98	
P-3	9.5	30	5	10	3	2	0.00	42.39	10.10	17.79	29.72	12.66	
P-4	2.5	15	5	17	2	2	0.00	29.20	26.00	5.72	39.07	28.98	
P-5	3.7	12	5	12	1	2	0.00	20.05	16.01	16.50	47.44	17.42	
P-6	7	12	1	16	2	1	0.00	7.51	32.68	11.29	48.51	8.16	
P-7	6	10	0	16	3	0	0.00	7.74	27.33	15.67	49.26	20.00	
P-8	22	20	5	24	1	3	1.85	3.98	36.49	14.46	43.22	34.39	

2) Small mammal sampling method :

We conducted 7 trapping sessions (April, May, June-July, August, September, October and February) in each of the 24 sampled hedgerows. For each of the 7 trapping sessions, seven days were necessary to sample all 24 hedgerows (in random order) so we can consider that the hedges were sampled simultaneously (dates of first trapping day for each session: 2003: 04/01, 05/13, 06/26, 08/07, 09/11, 10/21, 2004: 02/15).

We used a standardized method (Spitz et al. 1974) consisting of a 100 m line of 34 baited (wheat floor and margarine mixture and a piece of apple) live-traps spaced every 3 m and checked at dawn twice, that is, 24 hours and 48 hours after installation (2 trap-nights). Individuals captured at 24 hours were temporarily marked (colour mark on the tail) to avoid considering them twice if recaptured at 48 hours. Trapping is the most common method used to study small mammals (Gurnell and flowerdew 1990). It has been successfully used to detect patterns of richness, composition and abundance of small mammal communities through ecological gradients (Yu 1996). We used INRA live traps, a French model of live-trap, that are known to be very efficient in catching both shrews and rodents (Aubry, 1950). The total number of individuals trapped with this method (excluding recaptures at 48 hours) was used as an index of abundance for each species (Hansson 1967).

Eight species (rodents and shrews) were captured during the whole year of trapping. There were four rodents species: *Apodemus sylvaticus* (Wood mouse, As) (Linné 1758), *Clethrionomys glareolus* (Bank vole, Cg) (Schreber 1780), *Microtus agrestis* (Field vole, Mag) (Linné 1761), *Microtus subterraneus* (Common pine vole, Ms) (de Sélys-Longchamps 1836), and four shrew species: *Crocidura russula* (White-toothed shrew, Cr) (Hermann 1780), *Neomys fodiens* (Aquatic shrew, Nf) (Pennant 1771), *Sorex coronatus* (Common shrew, Sc) (Millet 1828), *Sorex minutus* (Pigmy shrew, Sm) (Linné 1766).

3) Data analysis :

Species richness (S) and Shannon index of diversity (H') were computed for each hedgerow and for each site (Shannon and Weiner 1949; Magurran 1988) using the "diversity" function of the "vegan" library (Oksanen et al., 2005) of the R statistical language (R 2.0.1, R Development Core Team, 2005).

Species abundances were expressed by total capture, without any correction, because the trapping effort was strictly the same for each trapping unit.

Discriminant analysis (Rao 1948) was computed on the table of Hellinger-transformed species abundances in the 24 hedgerows to highlight inter-site variability. This was computed using ADE-4 Software ™ (Thioulouse and al. 1997).

Multivariate analysis were performed using the R statistical language (R 2.0.1, R Development Core Team, 2005). Species abundance data were Hellinger-transformed to make them amenable for principal component analysis (PCA) and canonical redundancy analysis (RDA) (Legendre and Gallagher 2001). PCA and RDA were computed using the "rda" function of the "vegan" library (Oksanen et al. 2005). Variation partitioning was computed using a function written by Pierre Legendre in the R language, and now incorporated into the "vegan" library. A Venn diagram was made to present the variation partitioning.

The Minitab Software ™ (version 13.31) was used to perform regression analyses in order to link the coordinates of the 24 hedgerows on the first RDA axis with the total abundance of the species (sum over the seven trapping sessions).

Results

During the 11,424 trap-nights, a total of 1379 animals were captured during the whole year of trapping: 1191 (86%) were rodents and 188 (14%) were shrews. Total species abundances in each hedgerow are given in Table 2.3.

Table 2.3
Species captures (sum of the 7 trapping sessions) in the 24 hedges sampled in the 3 sites (BOC1. BOC2 and POL). The hedges sampled at each site are numbered 1 to 8. Species codes (columns) are given in the Materials and methods.
Total number of captures. mean number of captures. species richness (S) and Shannon's diversity (H') of the small mammal communities of the three sites are also given.

* Significant difference among abundances (mean number of captures) using the Mann-Whitney U-test ($p<0.05$)
** Significant difference among diversities (H') of the three sites using Hutcheson's test ($p<0.01$).

Hegdes	As	Cg	Ma	Ms	Cr	Nf	Sc	Sm	Total	Mean	S	H'
BOC1-1	12	0	1	13	7	0	7	4	44		6	2.313
BOC1-2	30	4	0	1	0	1	5	0	41		5	1.289
BOC1-3	10	3	1	0	0	0	1	1	16		5	1.627
BOC1-4	28	3	0	0	2	0	2	3	38		5	1.350
BOC1-5	23	8	1	0	2	0	2	5	41		6	1.854
BOC1-6	45	10	3	2	0	0	1	1	62		6	1.323
BOC1-7	60	6	0	3	2	0	3	1	75		6	1.143
BOC1-8	41	3	2	0	5	0	4	1	56		6	1.414
Site BOC1	249	37	8	19	18	1	25	16	373	46.62 (± 6.28)	8	1.75
BOC2-1	11	0	0	4	0	0	4	1	21		4	1.619
BOC2-2	32	0	0	0	7	0	1	1	41		4	0.976
BOC2-3	30	3	0	1	8	2	5	2	51		7	1.916
BOC2-4	33	22	1	0	1	0	2	3	62		6	1.578
BOC2-5	49	4	0	1	0	0	9	2	65		5	1.197
BOC2-6	20	4	1	0	8	0	4	0	37		5	1.792
BOC2-7	25	23	1	2	4	0	2	2	59		7	1.914
BOC2-8	28	2	2	0	7	0	11	4	54		6	1.971
Site BOC2	228	58	5	8	35	2	38	15	389	48.62 (± 5.35)	8	1.92
POL-1	30	6	0	3	4	0	7	1	50		6	1.868
POL-2	66	32	0	3	2	0	2	0	105		5	1.308
POL-3	63	22	0	5	0	0	3	0	93		4	1.259
POL-4	46	45	0	0	8	0	3	1	103		5	1.541
POL-5	32	10	0	4	1	0	1	0	43		5	1.482
POL-6	74	8	0	0	3	0	0	0	85		3	0.665
POL-7	49	3	0	0	2	0	0	0	54		3	0.535
POL-8	26	51	1	0	0	0	0	0	78		3	1.010
Site POL	386	177	1	15	20	0	16	2	617	77.12* (± 8.27)	7	1.41**

A discriminant analysis was performed to highlight inter-site variability: inter-site inertia was significant (*p=0.006*) and accounted for 18% of total variation in small mammal species abundances which permits us to make inter-site comparisons. The total and mean number of captures in hedgerows of BOC1 and BOC2 are quite similar whereas they are significantly higher in POL. Eight species were found in BOC1 and BOC2 but only seven in POL, due to the absence of the aquatic shrew Nf (*Neomys fodiens*). Only one individual of Nf was found in BOC1 and only two in BOC2, so the difference in total species richness is negligible among sites. The Shannon diversity index is the lowest in POL due to differences in species abundances among sites; the two main species, As (*Apodemus sylvaticus*) and Cg (*Clethrionomys glareolus*), were much more abundant in the Polder site. Whatever the sampling site, the dominant species was the wood mouse, *Apodemus sylvaticus* (As), which represented 67% of the total number of captures in BOC1, 59% in BOC2 and 63% in POL. The bank vole, *Clethrionomys glareolus* (Cg), was also well represented, particularly in POL with 29% of the total number of captures whereas it was only 10% and 15% in BOC1 and BOC2 respectively. The six other species were much more rare, always showing abundances smaller than 10%.

A principal component analysis (PCA) was performed on the Hellinger-transformed small mammal species abundances in the 24 hedgerows. The first principal component axis accounted for 42% of the variation in total species abundance. We used that axis as a global index of differentiation in community composition and plotted the values of the hedges along that axis on a map of the hedges (Fig. 2.1). In this representation, black squares (positive values) are opposed to white squares (negative values) in first PC axis values. The POL site (great majority of white squares) is opposed to the 2 bocages sites (majority of black squares). This figure also highlights intra-site variability: species abundance profiles may differ greatly among hedgerows within a site, whereas hedgerows from different sites could exhibit close assemblages. For example, POL-1 hedge (low small mammal abundance) is more similar with BOC1-1 or BOC1-8 than with other hedgerows of POL. BOC2-4 and BOC2-7 are closer to POL hedges than to other BOC2 hedges because of the high abundance of *C. glareolus*.

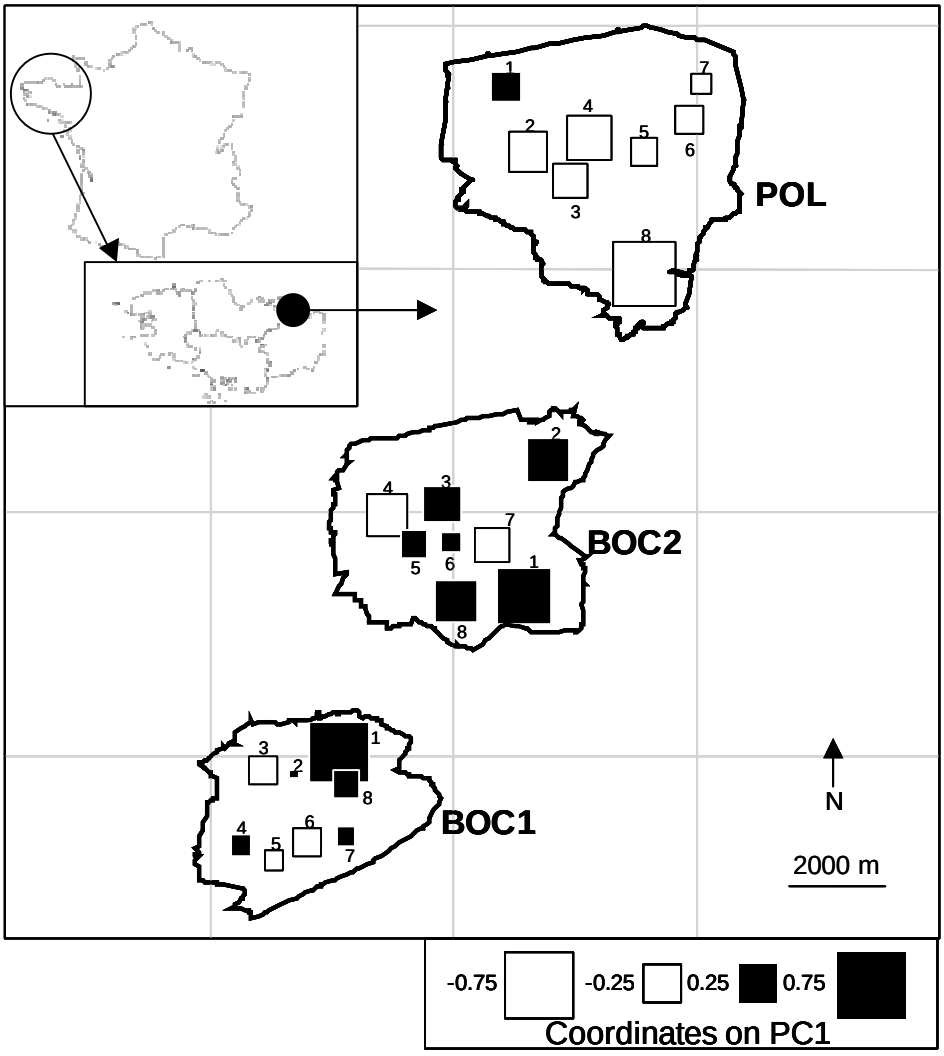

Fig. 2.1.
Map of the 24 sampled hedgerows. The size of the squares represent their values on the first principal component (which accounts for 42% of total variation) of the Hellinger-transformed small mammal species abundance data; open squares: negative values; black squares: positive values.

To identify the environmental variables that could explain these differences in species abundances among hedgerows, we performed a global redundancy analysis (RDA) of the Hellinger-transformed species abundance data constrained by the three group of variables (three scales: habitat, land-cover and landscape unit). The RDA biplot showing the species and the three groups of environmental variables is presented Figure 2.2.

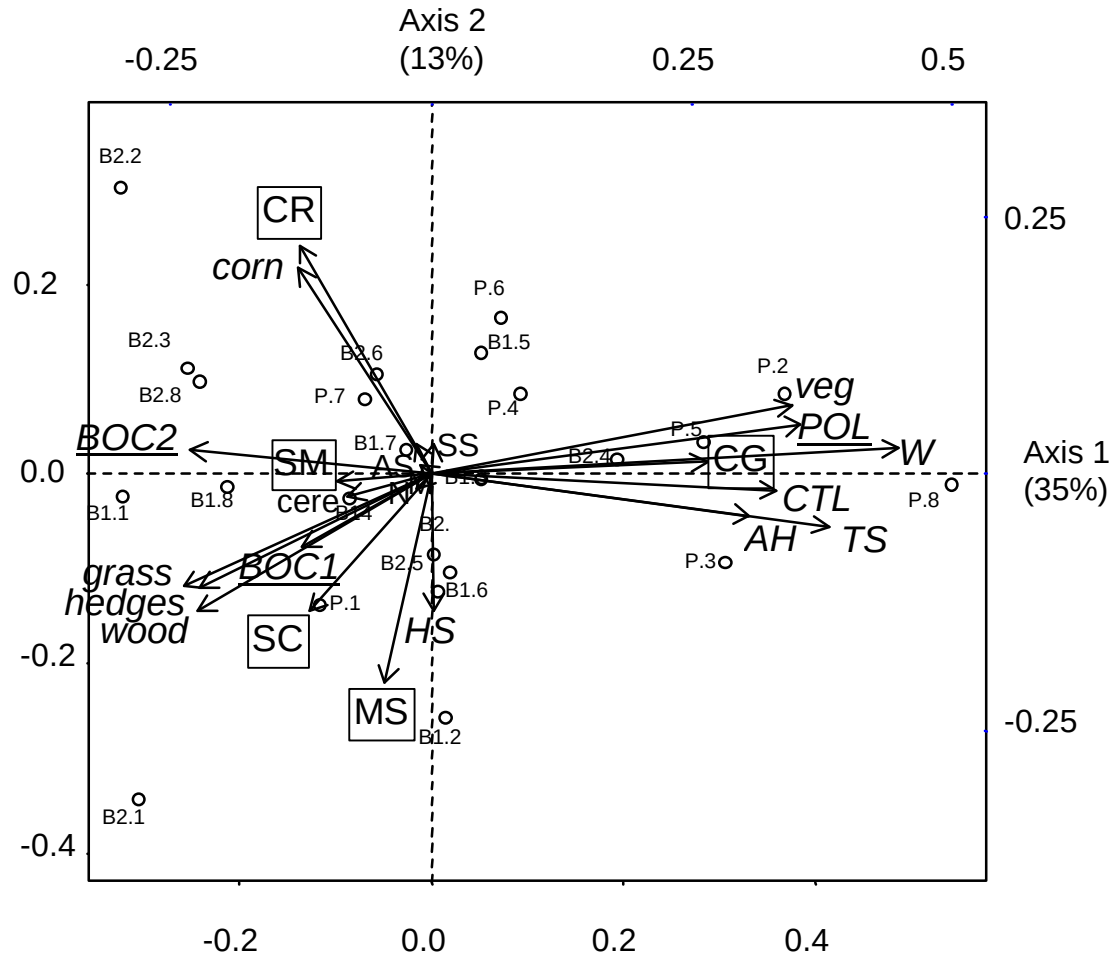

Fig. 2.2
Triplot of the species (squares), sites (small circles) and environmental variables on the two first canonical axis of the redundancy analysis ordination (Hellinger-transformed species abundance data constrained by the multi-scale environmental variables).

Symbols of the variables:
Habitat variables: W: width; AH: average height of the canopy; CTL: cover of the tree layer; TS: tree species richness; SS: shrub species richness; HS: herbaceous species richness.
Land-cover variables: veg: % vegetables; corn: % corn; cere; % cereals; grass: % grasslands; wood: % woods; hedges: density of hedges.
Landscape-Unit: BOC1: BOC1 site; BOC2: BOC2 site; POL: POL site.

The first canonical axis shows a clear opposition between (left) hedgerows adjacent to a high proportion of grasslands and woods and surrounded by a high density of hedges (most were BOC1 and BOC2 hedgerows), and, to the right, the largest and tallest hedgerows with a greater tree species richness, and surrounded by a high proportion of vegetable crops (most of them were POL hedgerows). Individual species are also associated with particular variables:

the Bank vole (Cg, *Clethrionomys glareolus*) is associated with hedgerows of great size (wide and high) and with high tree richness and cover from the POL site. The two *Soricidae* species, the Common shrew (Sc, *Sorex coronatus*) and the Pygmy shrew (Sm, *Sorex minutus*) are opposite to Cg along the first canonical axis; they are closely associated with BOC1 and BOC2 and with a neighbourhood of grasslands, woods, and hedgerows. The abundance of the White-toothed shrew (Cr, *Crocidura russula*) is correlated to the proportion of corn around the hedgerows. The Common pine vole (Ms, *Microtus subterraneus*) is associated with hedgerows with high herbaceous species richness. The Wood mouse (As, *Apodemus sylvaticus*, which is the dominant species at all three sites), the Field vole (Mag, *Microtus agrestis*) and the Aquatic shrew (Nf, *Neomys fodiens*) are not associated with any particular environmental variable.

The coordinates of the 24 sampled hedgerows along the first RDA axis can be linked to the species abundances (Fig. 2.3). Along the gradient defined by the first axis, we observe a significant increase of *Clethrionmys glareolus* (Cg, $p < 0.001$), and a significant decrease of *Crocidura russula* (Cr, $p = 0.007$) and *Sorex coronatus* (Sc, $p = 0.02$). The dominant species, *Apodemus sylvaticus* shows no significant tendency at the 5% significance level like the other four species (not shown).

To identify the more important explanatory variables and arrange them in a hierarchy, we performed separate redundancy analyses for each group of variables (the habitat variables, then the land-cover variables, and finally the landscape unit variables) with forward selection method. This selection gave as significant variables the hedge width and tree species richness (habitat group), the percentage of vegetables (land-cover group), and the site POL (landscape unit group). Then, using only the selected variables, we performed a variation partitioning analysis (Borcard et al., 1992; Borcard and Legendre, 1994). Graphical representation (Venn diagram) of the results is given in Figure 2.4. The two habitat variables explain the greater part of the variation in small mammal community composition (24.7%, adjusted R-square) whereas land-cover and the landscape unit POL totally overlap and account for less variation

(13.2%, adjusted R-square). 6.4% (adjusted R-square) of the variation is common to the three groups of variables.

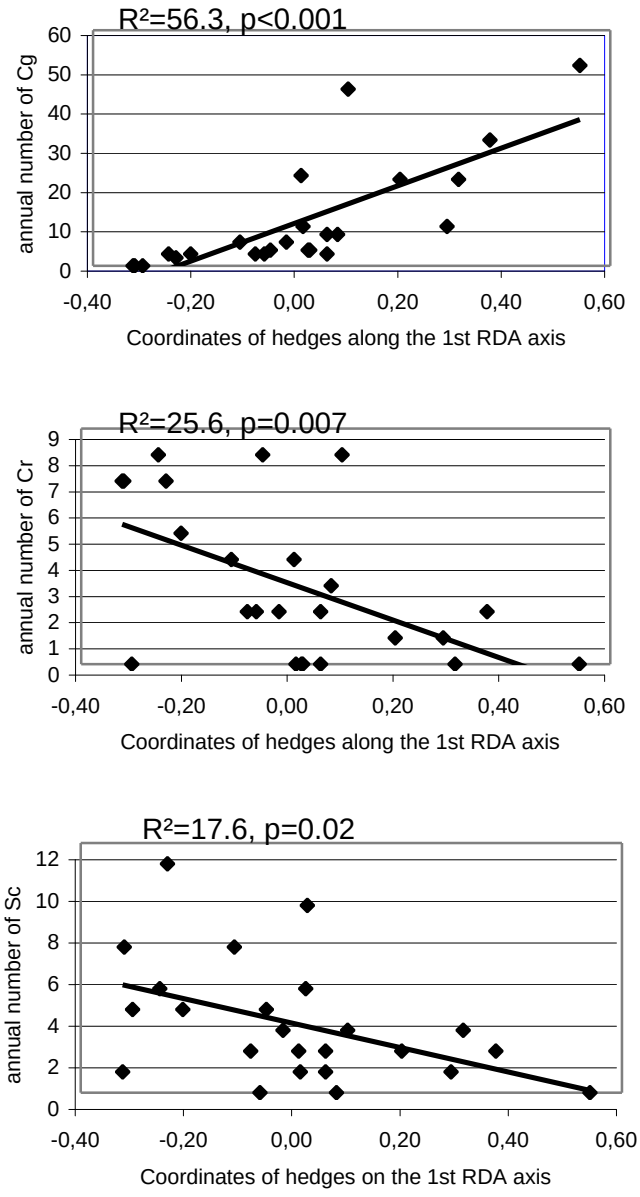

Fig. 2.3.
Relation between the total abundances (sum over all trapping sessions) of Cg (*Clethrionomys glareolus*), Cr (*Crocidura russula*), and Sc (*Sorex coronatus*) and the coordinates of the hedgerows along the 1st axis of the canonical redundancy analysis ordination (RDA Fig. 2.2).

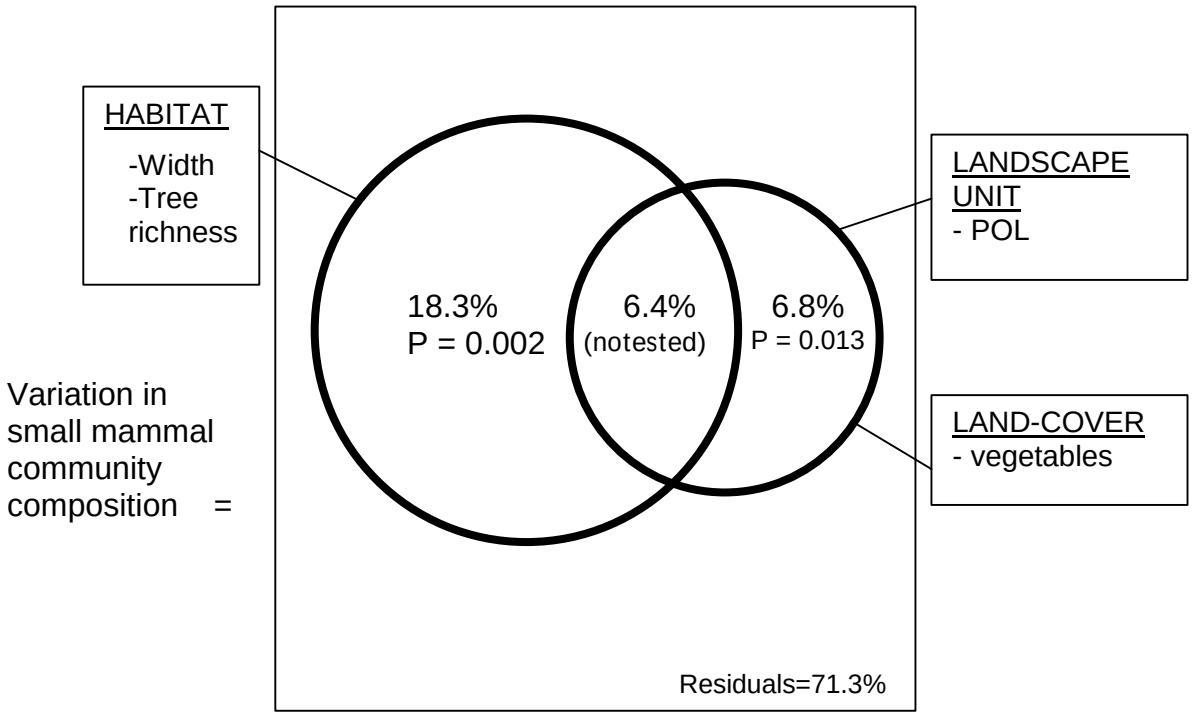

Fig. 2.4.
Venn diagram partitioning the variation of the small mammal community composition between forward-selected environmental variables of habitat, land-cover and. landscape units. The reported values are adjusted canonical R-squares. The circle for land-cover and landscape unit totally overlap.

Discussion

This study reveals that small mammal species assemblages exhibit spatial variability among hedgerows of three contrasted farming landscapes. Differences were observed on small mammal abundance and diversity among the three sites, showing a major difference between the most intensified site, POL, with the highest local small mammal abundance and the lowest diversity, and the two other sites, BOC1 (slightly intensified) and BOC2 (moderately intensified), with the lowest abundance and the highest diversity. Small mammals are a group of species where landscape configuration has been thought to strongly influence population dynamics (Hansson 1977; Barrett and Peles 1999). Raoul et al. (2001) showed that the stability of small mammals could be influenced by the proportion of grasslands in the landscape. Bowman et al. (2001) and also found that landscape context was related to the abundance of several species. Generally, in farming landscapes, loss of diversity is observed with agricultural intensification; Millan de la Pena et al. (2003) found similar results in a gradient of twelve sites differing by their level of agricultural intensification: species assemblages were different among sites, with a reduction of diversity. Moreover, isolated patches of habitat (this is the case in POL) usually contain fewer species than do less isolated patches because of increased extinction rates or decreased colonization rates (MacArthur and Wilson 1967; Rosenzweig 1995).

But among-site variability only accounts for 18% of the total small mammal assemblages variation. Differences among hedgerows are much more important that differences among sites. A fundamental question in population and community ecology is: what factors determine the distribution and abundance of species within local regions. Here, the question is to know which environmental variables are predominant to explain differences in species abundances among hedgerows. In a same landscape unit, we show that geographically close hedgerows may exhibit very different patterns of species abundances. This is in accordance with the findings of Bowman et al. (2000) where small mammal populations can exhibit heterogeneous densities over relatively short distances, i.e. hundreds of meters (like in our sites). This suggests the contribution of local processes in addition to landscape processes. For example, Bryja and Zukal (2000) demonstrated in a same landscape, that the small mammal community in newly planted corridors was very different from fully

developed windbreaks. Canova and Fasola (1991) also showed that community diversity was correlated with habitat structural diversity.

Whatever the hedgerow, the two most abundant species were the Wood mouse (*Apodemus sylvaticus*) and the Bank vole (*Clethrionomys glareolus*) which are known to be associated with woodland habitat (Canova and Fasola 1991; Douglass et al. 1992). According to the RDA analysis, *Apodemus sylvaticus* seems not to be influenced by any of the environmental variables we considered. This species is very ubiquitous and eurytopic with a wide ecological plasticity (Butet 1984) and can demonstrate shifts in habitat occupancy (Ouin et al. 2000). Even if *Apodemus sylvaticus* is dependent on the hedge habitat, particularly in the autumn and winter seasons (Pollard and Relton 1970), it appears that it is free to use the whole field and thus to occupy a two-dimensional (hedgerows and agricultural mosaic) rather than an essentially one-dimensional range (hedgerows). Consequently, the generalist nature of *Apodemus sylvaticus* may enable them to adapt to changing countrysides better than other species with more specialized habitat requirements (Love et al. 2000).

Contrary to *Apodemus sylvaticus*, the Bank vole, *Clethrionomys glareolus* is known to be restricted to hedgerows in farming landscapes, not moving far into adjoining fields (Kosakiewicz 1993). For such a habitat specialist species, abundance in a habitat patch may potentially depend on many different local or landscape factors, like the patch size, patch quality (e.g. shelter), and patch isolation, determined by characteristics of the landscape (structural connectivity), such as the amount of favourable habitat surrounding the patch. In our case, local habitat characteristics seem to have a great influence on *C. glareolus* abundance: wide and high hedgerows with a great woody character (high cover of the tree layer and high tree species richness) host high abundances of bank vole even if patch isolation is important (low connectivity); in POL, *C. glareolus* seems to be concentrated in the few hedgerows of the site, creating high population density. Nevertheless, Paillat and Butet (1996) showed that in this landscape unit, POL, *C. glareolus* were more abundant and stable in the hedges the less isolated.

The two other species of rodents were much more rare that the former. This seems to be logical because *Microtus agrestis* and *Microtus subterraneus* occur primarily on grassy and open habitats such as meadows (Innes and Millar 1994) and are more seldom encountered in hedgerows.

Relatively little attention has been paid to the influence of surrounding land-use patterns on small mammal populations. Arable fields are by their nature unstable habitats for

small mammals, particularly after harvesting, providing little cover from predators (Tew and Macdonald, 1993), but when cover is sufficient, they could provide additional resources. Concerning shrews, the abundance of *Crocidura russula* was correlated to the abundance of corn around hedgerows. It is the commonest shrew species in Western Europe, probably due to its ability to live in open habitat and its capacity to colonize agricultural fields (Genoud and Hutterer, 1990). It has been shown to be less sensitive to agricultural intensification than other shrews (Millan de la Pena et al., 2003). Corn exhibiting a dense and high cover during part of the year could allow *Crocidura russula* to forage and exploit invertebrates resources in fields, especially because less insecticide is used in corn fields than in cereals (Millan de la Pena et al., 2003b). On the contrary, the two species of *Soricidae, Sorex coronatus* and *Sorex minutus* are much more strongly associated with undisturbed habitats around the hedgerows, such as woods, grasslands, or hedges. They are known to be dependent on preserved habitats and densely wooded landscapes (Taberlet, 1986); that is possibly why they are more abundant in the hedgerows of BOC1 and BOC2.

The variation partitioning analysis gave hedges width and tree species richness of the hedgerows as the predominant explanatory variables, explaining the demographic structure of the small mammal community, and especially the predominance of *Clethrionomys glareolus*. Several studies have shown, on the contrary, higher densities of small mammals in small compared to larger patches (Diffendorfer et al., 1995; Nupp and Swihart, 1996). Habitat quality is strongly influenced by the availability of resources (theoretically enhanced by patch size) and the risk of predation (Lin and Batzli 2001). Small mammals in many communities show preference for habitats with high vegetation cover (Kotler and Brown, 1988), a fact that is closely related with the perceived predation risk (Bowers, 1988; Diaz, 1992; Lagos et al., 1995). Living in a habitat with dense and thick vegetation is considered to be an antipredatory strategy against both aerial (Longlang and Price, 1991) and terrestrial predators (Jedrzejewska and Jedrzejewski, 1990). Moreover, we could make the hypothesis that a wide patch could limit the predation pressure by diminishing the edge effect.

The landscape unit POL and the proportion of vegetables in crop fields surrounding the hedgerows are also shown in the variation partitioning results to have a role in structuring the community. They totally overlap because vegetables are quite rare in the two other sites. Additionally to habitat characteristics, landscape is known to have impact on small mammal communities (Hansson, 1977; Barrett and Peles, 1999): due to its history and particular

features, the POL landscape unit contributes to a particular structure of the small mammal community. The selection of the proportion of vegetables as a significant explanatory variable is only a consequence of the particular land-cover in POL which does not seem to have any ecological significance for *Clethrionomys glareolus*. It could have the role of a resource for species foraging in the agricultural mosaic such as *Apodemus sylvaticus,* but this is not the case of *C. glareolus*.

Conclusion :

Landscape and local habitat characteristics played a major role in structuring the small mammal community in our three study sites, with a predominance of local habitat variables. Microhabitat features and, to a lesser extend, landscape characteristics determined the composition and dynamics of the small mammal assemblages.

For preserving small mammal diversity in agricultural landscape, preservation of dense hedgerow networks is crucial, particularly for species restricted to these semi-natural linear elements. Moreover, additionally to quantity of habitat, hedgerow quality play a major role by allowing hedges to host a greater abundance of small mammals.

Future investigations will be carried out on hedgerow management by the farmers which could influence seed and berry production as well as insect availability in arable hedges inducing fluctuations in rodent and shrew populations.

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CHAPITRE 3

CHAPITRE 3

Seasonal changes in a small mammal community from hedgerows of contrasted agricultural landscapes in Western France

MICHEL Nadia, BUREL Françoise, LEGENDRE Pierre, BUTET Alain

Soumis à ECOSCIENCE

Dynamique saisonnière du paysage (années 1997/1998)(Photos : Yann Rantier)

Seasonal changes in a small mammal community from hedgerows of contrasted agricultural landscapes in Western France

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Runnig title : Seasonal changes in a small mammal community

Abstract

In this paper, we studied the seasonal variations of abundance in a community of small mammals living in hedgerows, in three contrasted landscapes of Western France differing by their level of land-use intensity and hedgerow network density (BOC1: slightly intensified; BOC2: moderately intensified and POL: highly intensified). We hypothesized that different levels of agricultural intensification could induce different seasonal patterns of the community and the component species, and/or different intensities of the temporal fluctuations.

We showed that the temporal structure of the species abundances was the same whatever the sampling unit and whatever the landscape unit considered, showing that the seasonal patterns of the small mammal assemblages were not affected by agricultural intensification. On the other hand, the amplitude of abundance fluctuations was the highest in the more intensified site (POL), and was the smallest in the more stable and preserved site.

Species exhibited specific seasonal variations, underlying a clear opposition between on the one hand the months of summer, were the majority of species (except the dominant one, the Wood mouse, *Apodemus sylvaticus*) presented their highest abundances, and on the other hand the months of spring, autumn and winter were the Wood mouse was numerous and dominant. This particular seasonal pattern of the Wood mouse was observed during several years and was in accordance with the literature: this pattern was explained by its ability to leave hedgerows for exploiting cultivated fields in summer when crops present sufficient cover.

Keywords

abundance; agricultural intensification; *Apodemus sylvaticus*; community; diversity; farming landscape; seasonal variations; small mammals

Introduction

The increasing land use by humans 1000 years ago was a fundamental event for the development of a high level of species biodiversity in Central Europe (Priorr 2003). Nowadays, arable farming is one of the most widespread forms of land use in Europe (Stoate et al., 2001). Over the last decades, drastic changes have occurred in agricultural methods, practices, and policies leading to changes in farming landscape structure and composition. Current land use techniques are said to be responsible for a decline in habitat diversity for many species of flora and fauna in rural landscapes (Buchs 2003), leading to a widespread loss of biodiversity; these declines have been reviewed by Robinson and Sutherland (2002), Stoate et al. (2001), and McLaughlin and Mineau (1995) for many groups of animals and plants. In Western France like in the rest of Europe, enlargement of parcel sizes has occurred, associated with a wide decline in semi-natural elements such as woodlots and hedgerows (Morant, 1999; Baudry and Jouin, 2003). Areas devoted to agricultural fields have also increased to the detriment of natural meadows (Burel and Baudry, 1990).

In current farming landscapes, the remaining semi-natural elements play a major role in maintaining biodiversity due to their stability in time in the mosaic of cultivated fields (Forman, 1995 ; Marshall et Arnold, 1995 ; Kleijn et Verbeek, 2000 ; Freemark et al., 2002; Deckers et al. 2004). Hedgerows, in particular, play an essential role in farming landscapes by preserving biodiversity, a role that goes beyong the aesthetical aspects and protection against wind and erosion (de Blois et al., 2002): they serve as habitat for specialist species (Forman and Baudry, 1984; Paillat and Butet, 1996) and seasonal refuges for species able to temporarily colonize the agricultural matrix (Morvan et al., 1994; Delettre et al., 1998), or they are used as dispersion corridors among woody patches (Duelli et al., 1990; Petit and Burel, 1998b).

Small mammals (rodents and shrews < 40g) are common features of rural landscapes, and for most of them, hedgerows serve as permanent habitat even if some species are also able to temporarily exploit agricultural fields that offer sufficient cover, e.g. corn (Burel, 1996). Small mammals are often considered as important pests of agricultural products, both in the field and in storage (Leirs 1993), and vectors of diseases (Skinner and Smithers 1990).

Ecologically, small mammals have a significant impact on the environment as grazers, seed eaters, and insectivores; they also play a fundamental role as prey to avian and terrestrial predators (Kern 1981; Linzey and Kesner 1997a,b). They are also useful indicators of environmental conditions as their populations respond rapidly to environmental changes (IN176 Linzey and Kesner 1997a,b), underlining the value of long-term studies of small mammals. There are a lot of studies of small mammals in patchy agricultural habitats (Geuse et al., 1985; Gottfried, 1979; Wegner and Merriam, 1979; Middleton and Merriam, 1981; Fahrig and Merriam, 1985; Szacki, 1987; Gliwicz, 1988), but few studies have investigated seasonal variations in small mammal community composition and structure (Ylonen et al., 1991; Brady and Slade, 2004). Those studies showed that species composing the community exhibited different temporal patterns and that exchanges could be possible between permanent habitats and the surrounding agricultural matrix as a function of the season and the species considered. In fact, most field studies consider only small mammal densities during the breeding season, giving an incomplete picture about the dynamics of the small mammal communities (Ylonen et al., 1991).

Paillat (2000) and Butet et al. (in press) studied the one year seasonal variations of a small mammal community in permanent habitat patches of the field boundary network in an highly intensified agricultural landscape. They found that the structure of the small mammal community changes along the year according to species fluctuations. But this study was conducted in a single site, not permitting to detect effects of agricultural intensification on temporal patterns of the community.

In the present study, we used three landscape units differing by their level of agricultural land-use intensity and hedgerow network density where we trapped small mammals in hedgerows, and studied the seasonal variations of the community composition and structure. A preliminary study has shown that these three sites differed with respects to the diversity and abundance of the small mammal species, using cumulative data for the whole year of trapping (Chapter 1: Michel et al (in press), Chapter 2: submitted paper). So we make the hypothesis that differences in agricultural intensity among the study sites could influence the intensity of the abundance fluctuations or the temporal structure of the community. We also aimed to determine which are the species the more responsible for the fluctuations, and what are the seasonal patterns of the different species composing the community.

Materials and methods

1) Study sites :

The study area was located in Western France, south of the Mont Saint-Michel Bay (48° 36' N, 1° 32' W). Three landscape units were chosen in the "Site Atelier de Pleine-Fougères" which is an area where several studies have been conducted on the response of biodiversity to agricultural intensification (Burel et al. 2004). The three sites, called BOC1, BOC2 and POL, differ by their level of land-use intensity and hedgerow network density. BOC1 is an agricultural landscape locally named "bocage". It is known to be the least intensified of the three sites, with only 36% of its UAA (Used Agricultural Area) devoted to cultivated fields, versus 64% of grasslands. The hedgerow network is the densest in BOC1 with a density of 98 m/ha. In BOC2, agriculture intensity is higher than in BOC1, with 64% of the UAA covered by crop fields (versus 36% of grasslands), and a hedgerow network density of 48 m/ha. Finally, POL is an area reclaimed from the sea; it is structured by a network of dykes, and is the most intensified site, with 91% of the UAA devoted to cultivated fields and only 12 meters of hedgerows per hectare. The areas of these landscape units are 1019 ha for BOC1, 1659 ha for BOC2, and 2544 ha for POL. They were distant of 2100 m between BOC1 and BOC2, 2900 m between BO2 and POL, and 10300 m between BOC1 and POL. At each site, 8 hedgerows were chosen along the network to become sampling units for trapping small mammals. They were chosen as distant as possible from one another, with 600 m minimum distance between hedges in BOC1 and 700 m in BOC2 and POL.

2) Data collection :

We conducted 7 trapping sessions during the year 2003/2004 (April, May, June-July, August, September, October 2003 and February 2004) in each of the 24 hedgerows. For each trapping session, one week was necessary to sample all 24 hedgerows (in random order). For all practical purposes, we can consider that the hedges were sampled simultaneously (dates of first trapping day for each session: 2003: 04/01, 05/13, 06/26, 08/07, 09/11, 10/21, 2004: 02/15).

We used a standardized method (Spitz et al., 1974) consisting of a 100 m line of 34 baited (wheat floor and margarine mixture and a piece of apple) live-traps placed every 3 m, and checked at dawn twice, that is, 24 hours and 48 hours after installation (2 trap-nights). Individuals captured at the first visit (24h) were temporarily marked (colour mark on the tail) to avoid considering them twice if recaptured at the second visit. Trapping is the most common method used to study small mammals (Gurnell and flowerdew, 1990). In particular, live trapping is a powerful technique with which to carry out monitoring for multiple species (Flowerdew et al. 2004). It is an established technique incorporated into a variety of ecological studies (Southern, 1965; Southern and Lowe, 1982; Healing 1980; Johnson et al., 2002), for example to detect patterns of richness, composition, and abundance of small mammal communities across ecological gradients (Yu, 1996). We used INRA live traps (a French live-trap model) that are known to be very efficient in catching both shrews and rodents.

For the dominant species of the community, *Apodemus sylvaticus*, abundance data were also available for two other years of trapping (1995/1996 and 2004/2005) in the POL site; this allowed us to make inter-annual comparisons for the abundance of that species (1995: INRA live-traps; 2004: UGGLAN live-traps).

3) Data analyses :

Community composition data (species abundances) were subjected to the Hellinger transformation before multivariate analyses. The Hellinger transformation permits to make species abundance data amenable to canonical redundancy analysis (RDA) in particular (Legendre and Gallagher, 2001).

The Hellinger-transformed community composition data were used to perform multivariate analysis of variance. For each site, we first tested the time-space interaction potentially structuring the pattern of species abundances. That first step was necessary before testing the significance of the temporal variation of the trapping results. The analysis was performed within each of the three sites and also after combining the three sites for a total of 24 hedgerows. A two-way analysis of variance without replication is equivalent to a multiple regression using binary dummy variables (1 or 0) to code for space, time, and interaction; but using a code of binary variables leaves no degrees of freedom to test the space-time

interaction. That problem was solved by using a more parsimonious way of coding for time (Legendre et Borcard, 2005): we used PCNM (Principal Coordinate of Neighbour Matrices) base functions (Borcard and Legendre, 2002) for coding the sampling dates. PCNM functions represent a spectral decomposition of the temporal relationships among sampling dates, and are fewer in number than binary variables coding for the same set of dates (Borcard et al., 2004): only 3 PCNM functions were necessary to code for the 7 trapping sessions. The hedges within each site were coded using Helmert contrasts (Chambers and Hastie, 1992); 7 contrasts were necessary to code for the 8 hedges. We then computed the space-time interaction variables as the products of all space-coding dummy variables (7) by all time-coding PCNM base functions (3): 21 product variables were necessary to code for the interaction. That left (8*7-1-7-3-21)= 24 degrees of freedom in the denominator of the F-statistic for the test of the space-time interaction. The interaction, then the space and time main factors, were tested for significance by canonical redundancy analysis (RDA) following Legendre and Anderson (1999). RDA was computed using the “rda” function of the “vegan” library (Oksanen et al., 2005) of the R statistical language (R Development Core Team, 2005).

The Shannon index of diversity was calculated for each sampling date using the “diversity” function of the “vegan” library (Oksanen et al., 2005) of the R language.

The possible effect of season on species abundances and diversity was tested using a non-parametric alternative to two-way analysis of variance without replication, the Friedman test, using the “friedman.test” function of the R language (seasonal effect on *Neomys fodiens* was not tested because of its too low abundance: 1 capture in BOC1 and 2 captures in BOC2 during the whole year of trapping).

Finally a canonical redundancy analysis (RDA) was performed on the Hellinger-transformed species abundance data constrained by trapping session months, showing the trajectory of changes in community composition along time. RDA was computed using the “rda” function of the “vegan” library of R (Oksanen et al., 2005).

Results

The study was based on a total of 1379 captures during the 2003/2004 trapping year. Eight species (rodents and shrews) were captured during the whole year of trapping. Four rodents species were found, representing 86% of the captures: *Apodemus sylvaticus* (63%) (As, Wood mouse) (Linné 1758), *Clethrionomys glareolus* (20%) (Cg, Bank vole) (Schreber 1780), *Microtus agrestis* (1%) (Ma, Field vole) (Linné 1761), *Microtus subterraneus* (3%) (Ms, Common pine vole) (de Sélys-Longchamps 1836), and four shrew species, representing 14% of total captures: *Crocidura russula* (5%) (Cr, White-toothed shrew) (Hermann 1780), *Neomys fodiens* (<1%) (Nf, Aquatic shrew) (Pennant 1771), *Sorex coronatus* (6%) (Sc, Common shrew) (Millet 1828), *Sorex minutus* (2%) (Sm, Pigmy shrew) (Linné 1766).

The space-time interaction terms of the multivariate analyses of variance were not significant (Table 3.1). This allowed us to interpret the results of the tests of the main factors, time and space. These factors both had a significant effect in structuring the small mammal community within each site and in the analysis of the three sites combined. The present study focuses only on the temporal structure of the community to highlight seasonal variations in species abundances.

Table 3.1.
Permutational probabilities (999 permutations) resulting from the multivariate analysis of variance among the sampling dates (in the form of PCNM base functions), space (in the form of Helmert coding) and time-space interaction (product of all time and space coding variables) on the Hellinger-transformed species abundance data.

	Time	Space	Interaction
BOC1	0.002 **	0.007 **	**0.93 n.s.**
BOC2	0.003 **	0.007 **	**0.79 n.s.**
POL	0.001 ***	0.016 **	**0.63 n.s.**
The 3 sites	0.001 ***	< 0.001 ***	**0.69 n.s.**

** 0.001 < p = 0.01, *** p = 0.001, n.s. = not significant

Fig. 3.1. presents the seasonal variations of the total abundance of the small mammals (all species pooled) in the three landscape units. For each site, we calculated the coefficient of variation (CV = 100 $s_x / \bar{x}$) which represent the relative dispersion. CV is the lowest in BOC1 with 31.6%, higher in BOC2 (62.8%), and the highest in POL with 71.2%.

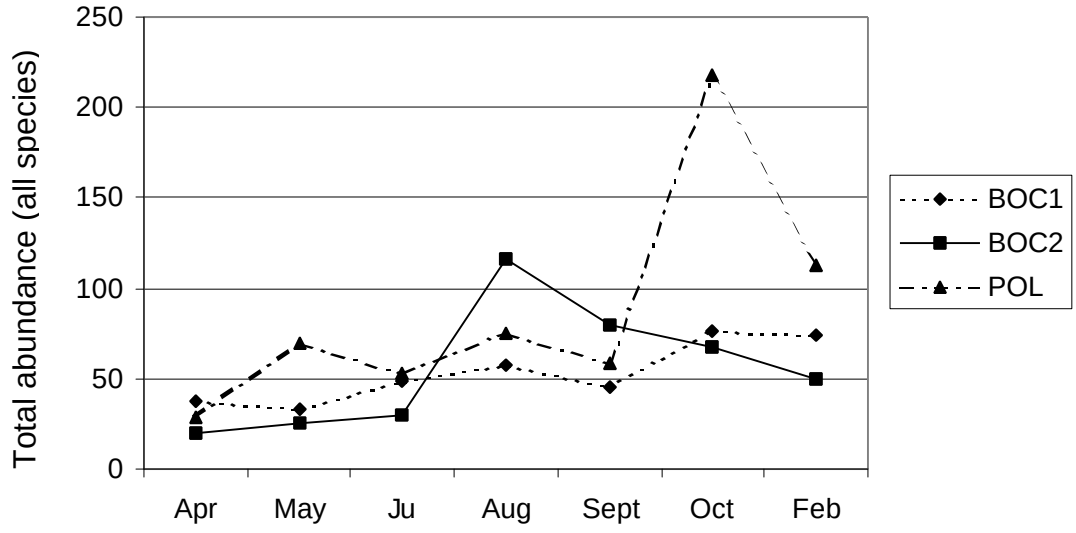

Fig. 3.1.
Seasonal variations of total abundance of the small mammal community in the three landscape units, BOC1, BOC2 and POL.

Seasonal variations of the Shannon index of diversity are presented Fig. 2.2A. Diversity responds significantly to the season effect at all sites (Friedman tests, Table 2.2): diversity was the highest in August and September due to a better distribution of the abundance of species during the summer (Fig. 2.2). In fact, except for the dominant species, the Wood mouse, *Apodemus sylvaticus*, all species present a progressive increase in captures from spring to summer and a decrease in autumn or winter (Fig. 2.2). *Apodemus sylvaticus* exhibits a particular seasonal profile, with a relative stability of captures in the spring, a reduction in summer, and an increase in autumn.

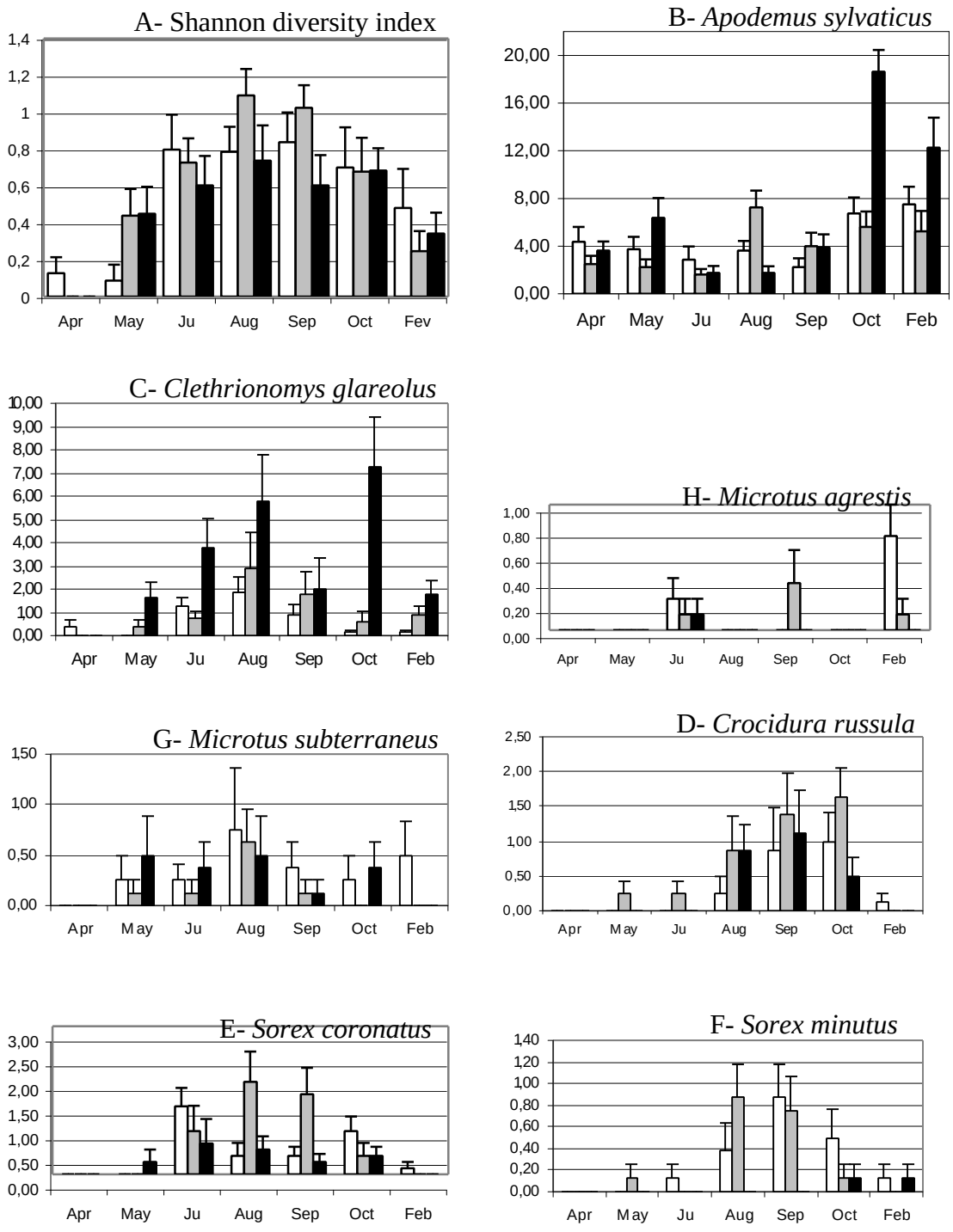

Fig. 2.2
Seasonal variations of (A) the Shannon diversity index per site (all hedges combined) and (B-H) species abundance (mean abundance per trap-line, all hedgerows combined) at the three sites (n = 8 hedges per site).

- BOC1
- BOC2
- POL

The seasonal effect on species captures, tested with Friedman tests, was significant at the three sites for *Apodemus sylvaticus*, *Clethrionomys glareolus*, *Crocidura russula*, *Sorex coronatus* (except in POL) and *Sorex minutus* (except in POL) (Table 2.2). The two *Microtus* species do not present significant inter-season variability (Table 2.2), probably because of their low abundances that did not permitting to detect seasonal effect; significance of *Microtus agrestis* in BOC1 may be a case of type I error due to the sporadic appearance of this generally rare species.

Table 2
Seasonal effect on Shannon diversity index and captures of each species at the three sites : Friedman's two-way anova by ranks (n = 8 per site) among the seven dates (d.f.= 6); (n = 8 hedges per site).

	BOC1			BOC2			POL		
	Chi²	*p*-value	Signif.	Chi²	*p*-value	Signif.	Chi²	*p*-value	Signif.
Diversity	16.58	0.001	**	27.56	<0.001	***	16.88	0.010	**
Apodemus sylvaticus	22.73	<0.001	***	14.62	0.023	*	37.00	<0.001	***
Clethrionomys glareolus	23.51	<0.001	***	12.71	0.050	*	24.8	<0.001	***
Microtus agrestis	25.12	<0.001	***	6.50	0.396	n.s.	6.00	0.423	n.s.
Microtus subterraneus	5.34	0.500	n.s.	11.06	0.098	n.s.	5.53	0.478	n.s.
Crocidura russula	19.99	0.009	**	23.19	<0.001	***	21.28	0.002	**
Sorex corontus	21.75	0.013	*	23.02	<0.001	***	7.70	0.261	n.s.
Sorex minutus	14.26	0.027	*	20.67	0.002	**	5.00	0.544	n.s.

* 0.01 < *p* = 0.05, ** 0.001 < *p* = 0.01, *** *p* = 0.001, n.s. = not significant.

A canonical redundancy analysis (RDA) was performed on the Hellinger-transformed species abundance data of the three sites together (24 hedgerows, 7 sampling dates, 8 species). The biplot presented in Fig. 3.3 show a clear opposition of the community composition between the summer months (June, August and September, left) where all species (except *Apodemus sylvaticus* and the very scarce species *Microtus agrestis* and *Neomys fodiens*) are well represented, and the other months (April, May, and February, right) characterized by a high dominance of *Apodemus sylvaticus.*

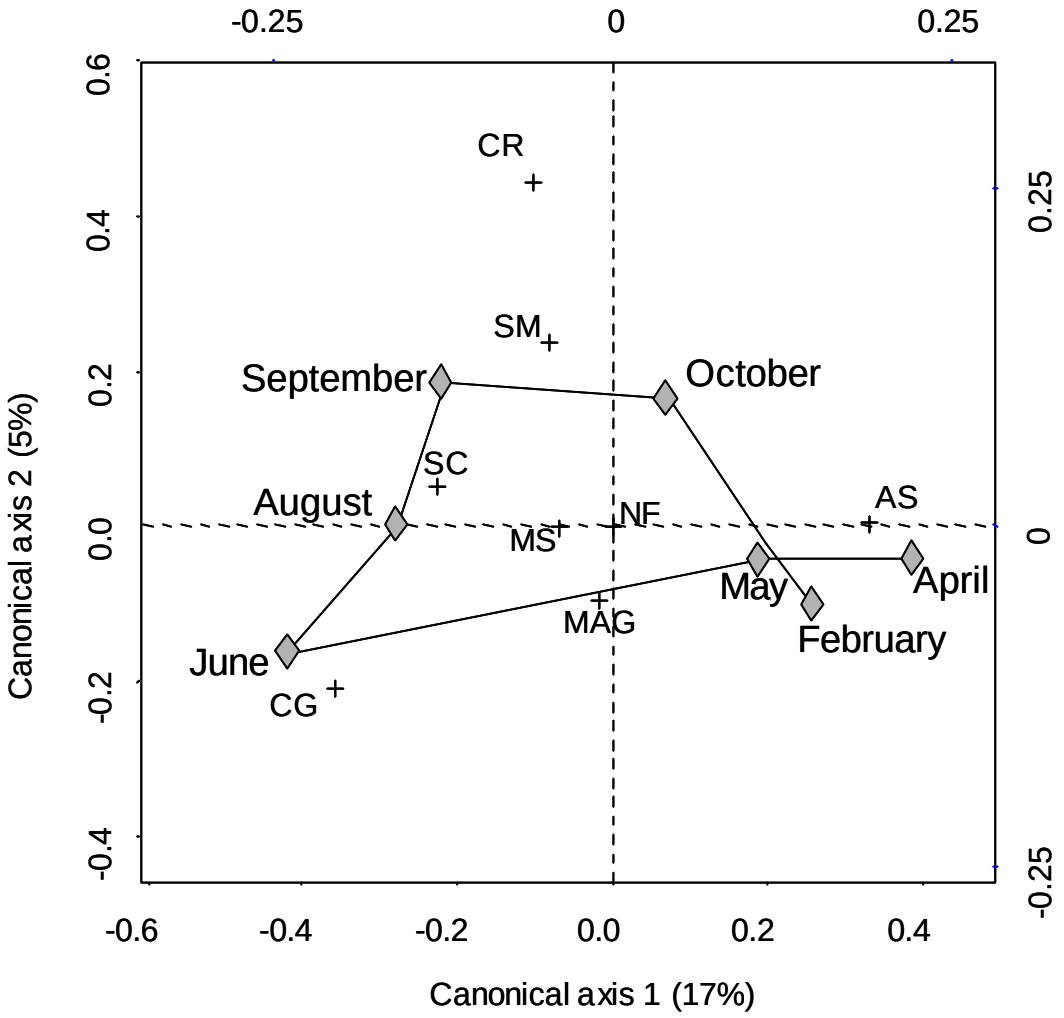

Fig. 3.3
First plane of the canonical redundancy analysis (24 sampling units by 7 trapping sessions, 8 species) showing the species and the trapping months. The months are connected by a line showing the trajectory of the community composition along time in the biplot.

Finally, for the most abundant species, *Apodemus sylvaticus*, we compared the months of minimum and maximum abundances during three sampling years: 1995/1996 (total of 320 *A. sylvaticus* captured during the whole year) , 2003/2004 (total of 386 *A. sylvaticus* captured) and 2004/2005 (total of 115 *A. sylvaticus* captured) (Table 3.3). The month of minimum abundance was always June, whereas the month of maximum abundance was always in autumn (October or November), showing a stability in the pattern of abundance of this species over the years. Mean number of captures was not significantly different among years in June (Friedman test, $p>0.05$) whereas it could vary among years in autumn ($p = 0.04$) (perhaps because of the use of different trap models), but the mean amplitudes were not significantly different over years ($p>0.05$).

Table 3.3
Inter-annual comparisons ?? (1995, 2003 and 2004) of the abundances of *Apodemus sylvaticus* at the POL site.

	Minimum	Maximum	Mean Amplitude	Coefficient of variation
1995 (INRA live-traps)	**June** ***2.13*** ± ***0.72***	**November** *15.25* ± *1.75*	*14.38* ± *1.18*	*76.24*
2003 (INRA live-traps)	**June** ***1.75*** ± ***0.59***	October ***18.63*** ± ***1.83***	*19.38* ± *1.97*	*91.62*
2004 (UGGLAN live-traps)	**June** ***0.17*** ±***1.00***	November ***7.33*** ± ***2.93***	*8.83* ± *2.80*	*87.57*
Friedman test	$Chi^2 = 3.52$ $p = 0.17$	$Chi^2 = 6.34$ $p = 0.04$	$Chi^2 = 5.33$ ***p* = 0.07**	

Discussion

In this study, we showed that the small mammal community composition in hedgerows of agricultural farming landscapes vary according to seasons.

We firstly wanted to test the space-time interactions because a significant interaction would have indicated that the temporal structures differed from hedgerow to hedgerow, or that the spatial structures differed from time to time; this paper does not, however, focus on the spatial variability in community composition among hedgerows. The absence of significant interactions indicated that the differences among trapping dates can be modelled in the same way at all points in space, that is to say, at all sampled hedgerows of a landscape unit or of the three units together. Temporal variability is a common finding is small mammal studies (Grant, 1976; Morris, 1984; Vickery et al., 1989). In hedgerow network landscapes, each species encountered in our community is known to exhibit moderate annual cycle (Saint Girons, 1976), which is very different to annual or pluri-annual demographic outbreaks observed in open-field landscapes (ex. *Arvicola terrestris*) (Giraudoux et al., 1997). The fact that the temporal structure of the community is the same for all studied hedgerows shows that the differences in agricultural intensity among the three study sites had no effect on the temporal structure of the species assemblage. Nevertheless, even if the temporal structure is not affected by site effects, the intensity of variation in species abundances seems to be influenced by landscape units: the coefficient of variation (CV) of the total abundance of the community was the smallest in BOC1, the site of slight agricultural intensity, whereas it was much higher in the two other sites, BOC2 and POL, which had the highest land-use intensity. Researchers have used the coefficient of variation to measure stability (May, 1973; Tilman, 1996; Doak et al., 1998); because CV measures the percentage variation around the mean, greater CVs imply lower stability (Tilman et al., 1998). The total abundance of the community would then be more stable in BOC1, which is also the more stable site in terms of the land-use dynamics due to the high percentage of area occupied by grasslands. On the contrary, the two other sites would be more unstable because of culture rotations implied by a high percentage of cultivated fields. Greater stability of the landscape dynamics would lead to a greater stability of the small mammal community. Moreover, a greater simplicity in the

small mammal community (lower diversity in POL) leads to a greater instability (Salamolard et al., 2000).

Rodent populations fluctuate with variations in environmental conditions. However, species with different life histories will exhibit different patterns of population growth under similar environmental conditions (Windberg 1998). As a result, fluctuations in the population structure of individual species will affect community structure as well (Wilson et al., 2004). Actually, community structure varies over time as a result of fluctuations in abundances of the component species (Brown and Heske 1990), leading to seasonal variations of diversity and to an opposition between summer and the other seasons as shown in our study.

Concerning the dominant species, *Apodemus sylvaticus*, the survey showed that, unsurprisingly, there were significant differences in its abundance in hedgerows among seasons. Abundance of *Apodemus sylvaticus* has been shown to be typically low during summer and high in autumn and winter (Flowerdew, 1985; Wilson et al., 1993; Butet, 1994) as it was confirmed by our study with inter-sites comparisons, and with inter-annual comparisons at the POL site showing the minimum captures in June and the maximum in autumn whatever the sampling year. This pattern was observed in different types of areas: forested (Flowerdew, 1985; Wilson et al., 1993; Fernandez et al., 1996), heathlands (Butet, 1994), or agricultural landscapes (Montgomery and Dowie, 1993; Rogers and Gorman, 1995; Kotzageorgis and Mason, 1997). Because of its wide ecological valence and significant agility, the wood mouse could demonstrate shifts in habitat occupancy (Viitala and Hoffmeyer, 1985). In mosaic farmland landscapes, Ouin et al. (2000) showed that *A. sylvaticus* switched from hedgerows to crop fields during summer, corroborating the findings of Loman (1991) and Fitzgibbon (1997) who concluded that dispersal of this species was promoted when the crop mosaic provided sufficient cover. In contrast, grass provides similar poor-quality habitat all year round and few mice are likely to leave hedges for grass fields (Montgomery and Dowie, 1993). This could explain the greater stability of the community in BOC1 where grassland is the dominant land-cover.

On the contrary, *Clethrionomys glareolus* lives strictly in woody habitats and is very dependent and confined to hedgerows in agricultural landscapes, rarely moving far from them (Pollard and Relton, 1970; Eldridge, 1971). While *A. sylvaticus* abandons hedgerows to crop fields in the summer, *C. glareolus*, breeding actively in hedgerows, becomes well represented in the community during this period. Moreover, POL seems to be the site where *C. glareolus* abundance fluctuations presents the highest amplitude. This could be linked to the greater

isolation of the POL hedgerows (the smaller connectivity: 12 m of hedgerows per hectare), as demonstrated by Paillat and Butet (1996) where a decreasing connectivity in this site leads to a greater fluctuation amplitude of *C. glareolus*.

The two *Microtus* species, *M. agrestis* and *M. subterraneus*, are more often regular inhabitants of open fields than hedgerows (Saint Girons, 1976) which could explain their very low abundance in our captures. Their habitat and diet requirements differ from those of *A. sylvaticus* and *C. glareolus* (Innes and Millar, 1994): they are mostly grass eaters associated with short grasslands (Hansson, 1971, 1985). Interspecific competition may also influence species assemblages at the level of habitats but Harris and Woollard (1990) showed that those species could co-exist if a sufficient diversity of habitats is available.

The multi-species community of shrews found in our study sites also raise questions about competition and coexistence amongst morphologically and ecologically very similar insectivores (Churchfield et al., 2004). The reduction of a species in one season may be due to interference competition with one or more larger species (Hanski and Kaikusalo, 1989). Actually, large species have longer starvation times than small species, and they are hence potentially able to use habitats with greater temporal variance in food availability (Hanski, 1985). In this way, *Sorex minutus*, which displays the lowest shrew abundance, would be limited by the presence of the larger and more abundant *Sorex coronatus*, itself limited by the increase of the larger *Crocidura russula* in autumn. *C. russula* is the commonest shrew species in Western Europe, characteristic of open landscapes. The fact that this species peaks late in autumn could be explained by its ability to colonize and exploit crop fields, probably during the summer (Genoud and Hutterer, 1990) when cover is sufficient. It is probably more adapted to use invertebrate resources from cultivated areas, whereas *Sorex coronatus* and *Sorex minutus* are known to be more strictly dependent on resources occurring in permanent habitats (Lovari et al., 1976; Böhme, 1978; Taberlet, 1986; Spitzenberger, 1990; Hutterer, 1990).

Finally, all species exhibited a strong decrease in abundance during winter. Obvious explanation for the strong winter declines in the rodent community are climatic conditions and predation (Ylonen et al., 1991). For shrews, winter mortality is not generally correlated with weather conditions (Dokuchaev, 1989; Sheftel, 1989) but depends primarily on food availability (Dokuchaev, 1989).

Conclusion

Following this study (i.e. one year), it appears that the temporal structure of the small mammal community in hedgerows was similar in the three sampling units, showing that the seasonal patterns of the small mammal assemblages were not affected by agricultural intensification. Nevertheless, the intensity of abundance fluctuations seems to be influenced by landscape dynamics: a more stable community was found in the most stable system. The dominant species, *Apodemus sylvaticus* was hypothesized to use different habitats of the landscape as a function of the season: it was very abundant in hedges in spring and autumn, and was hypothesized to shift in crop fields in summer. Other species, more restricted to hedgerows were the more abundant in summer. Inter-specific competition could also play a role in the seasonal structure of the community, particularly for shrews.

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CHAPITRE 4

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Response of two diurnal raptors, the Common Buzzard (*Buteo buteo*) and the Eurasian Kestrel (*Falco tinnunculus*), to agricultural intensity in three landscape units of Western France

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(article en préparation)

Buse variable (*Buteo buteo*) et faucon crécerelle (*Falco tinnunculus*)

Response of two diurnal raptors, the Common Buzzard (*Buteo buteo*) and the Eurasian Kestrel (*Falco tinnunculus*), to agricultural intensity in three landscape units of Western France

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Abstract

In front of agricultural intensification, there have been a wide decline in biodiversity. Several floral and faunal groups have been concerned by a reduction of abundance in farming landscapes. In this study, we focused on two diurnal raptor species, the Common buzzard (*Buteo buteo*) and the Eurasian kestrel (*Falco tinnunculus*). We carried out a one year survey of the abundance of these two species in several observation points in three agricultural landscapes of Western France. The three sites are known to be on a gradient of land-use intensity and hedgerow network density. We also made an estimation of the prey availability by trapping small mammals in hedgerows of the same sites. It appeared that the two species responded differently to agricultural intensification: the abundance of the Common Buzzard significantly decreased with the reduction of semi-natural elements such as hedgerows, woodlots and grasslands, as well as with the decrease of small mammal availability at the landscape scale. The abundance of the Eurasian kestrel showed the same tendency, but the correlation was not significant. We also showed that the Common Buzzard was very dependant to woody habitats, whereas the Eurasian kestrel was much more associated with grasslands.

Keywords

Agricultural intensification; farming landscapes; Common Buzzard; *Buteo buteo*; Eurasian kestrel; *Falco tinnunculus*; prey availability

Introduction

Agriculture is the dominant land-use throughout much of Western Europe, and a significant part of European biodiversity is associated with farmland habitats (Stoate et al., 2001). Major changes have occurred in farm management since the 1950s, partly in response to government policies and partly through technological advances, creating a complex array of factors that influences biodiversity (Robinson and Sutherland, 2002). Landscape diversity has declined in Europe during the period of agricultural intensification (Meeus, 1993), with a tendency to create the less heterogeneous and the simplest landscapes (Nassauer and Westmacott, 1987). The advent of the Common Agricultural Policy of the European Union has accelerated this degradation (Donazar et al., 1997; Potter, 1997; Suarez et al., 1997), leading to a widespread loss of uncultivated elements such as hedgerows, woodlots and ditches, and the replacement of a high proportion of grasslands by crop fields (Burel and Baudry, 1995).

Environmental problems entailed by modern arable management are now associated with changes in landscapes and plant and animal communities, and a deterioration in soil, water and air quality (Stoate et al., 2001). The widespread decline in farmland wildlife received attention first in the 1970s and early 1980s. But despite the acknowledged importance of long-term monitoring studies, there are relatively few such projects in Europe. Nevertheless, some taxonomic groups are well long-term studied, such as birds. The period of intensification of farm management coincides with the decline of many farmland bird species (Fuller et al., 1995). The ways by which agricultural intensification could have an effect on bird populations are diverse: they generally concern diminished food supply (Potts, 1986; Campbell et al., 1997; Evans et al., 1997; Brickle et al., 2000), less suitable nesting habitats (Wilson et al., 1997; Chamberlain et al., 1999) or direct mortality of birds by farming practices (Crick et al., 1994; Green, 1995). Leptich (1994) showed that raptors exhibited decreased abundance and lower diversity in areas highly developed toward agriculture.

The Common buzzard (*Buteo buteo*) seems to be recovering in Europe from low populations due to past persecution and pesticide effects, while the Eurasian kestrel (*Falco tinnunculus*) do not show similar positive trends (Hagemeijer and Blair, 1997). In intensively-cultivated areas, the populations of those two species may be regarded as important ecological indicators and the monitoring of their trends as an important conservation task (Boano and

Toffoli, 2002). Moreover, Newton (1997) showed that diurnal raptor species are good indicators of anthropization. Birds of prey usually select as foraging habitats the more profitable areas based on the availability of their main prey items (see review in Cody, 1985). Small mammals constitute the main food source for both species, the Common Buzzard (70 to 98 % of its diet (Génsbøl, 1988) and the Eurasian kestrel (to 95% of its diet (Génsbøl, 1988).

In this study, we aimed to make a direct comparison of abundances of the Common buzzard (*Buteo buteo*) and the Eurasian kestrel (*Falco tinnunculus*) among three landscape units differing by their level of land-use intensity and hedgerow network density. We hypothesized that abundances of each species could be different in the three sites, in response to the gradient of agricultural intensity, and that the two species could respond differently. We wanted to show which landscape elements could be important for the two species, by linking differences of land-cover in the landscapes and differences of abundances for the two raptors. We also aimed to link these abundances to small mammal availability in the hedgerow networks.

Material and methods

1) Study sites:

The study took place in Brittany (department of Ille-et-Vilaine), south of the Mont-Saint-Michel Bay (48° 36’ N, 1° 32’ W, North-Western France). Three landscape units were chosen in a study area named “Site Atelier de Pleine-Fougères” were several studies have been conducted on different biological models (Burel et al. 2004) in response to agricultural intensification. We based the unit delimitation on landscape structure drawn from aerial photographs. We took into account the grain size of the field mosaic, the density of hedgerow network, and the relative abundance of grassland vs. cropland. The three chosen sites are known to form a gradient of agricultural land-use intensity (Fig. 4.1) and hedgerow network density. The first landscape unit (BOC1) is locally called “bocage” (common landscape in Brittany, characterized by a dense hedgerow network). In BOC1, farming systems are exclusively oriented toward dairy production; 2/3 of the UAA (Used Agricultural Area) is covered by grasslands and fodder crops and milk cows predominate in the livestock. The second site, called BOC2, is also a “bocage”, but the hedgerow network density is reduced. BOC2 is more intensified than BOC1: agriculture is mainly oriented toward mixed dairy-cattle and some crop production, with 1/3 of the UAA covered by grasslands and fodder crops. Finally, the third landscape unit, called POL, is a polder, reclaimed from the sea area with a network of dykes with few hedgerows. It is highly intensified with 90% of the UAA being crop fields; agriculture is oriented toward cereals and vegetables production. Hedgerow network densities were 98 m/ha in BOC1, 48 m/ha in BOC2, and 12 m/ha in POL. The landscape unit areas are respectively 1019 ha for BOC1, 1659 ha for BOC2, and 2544 ha for POL.

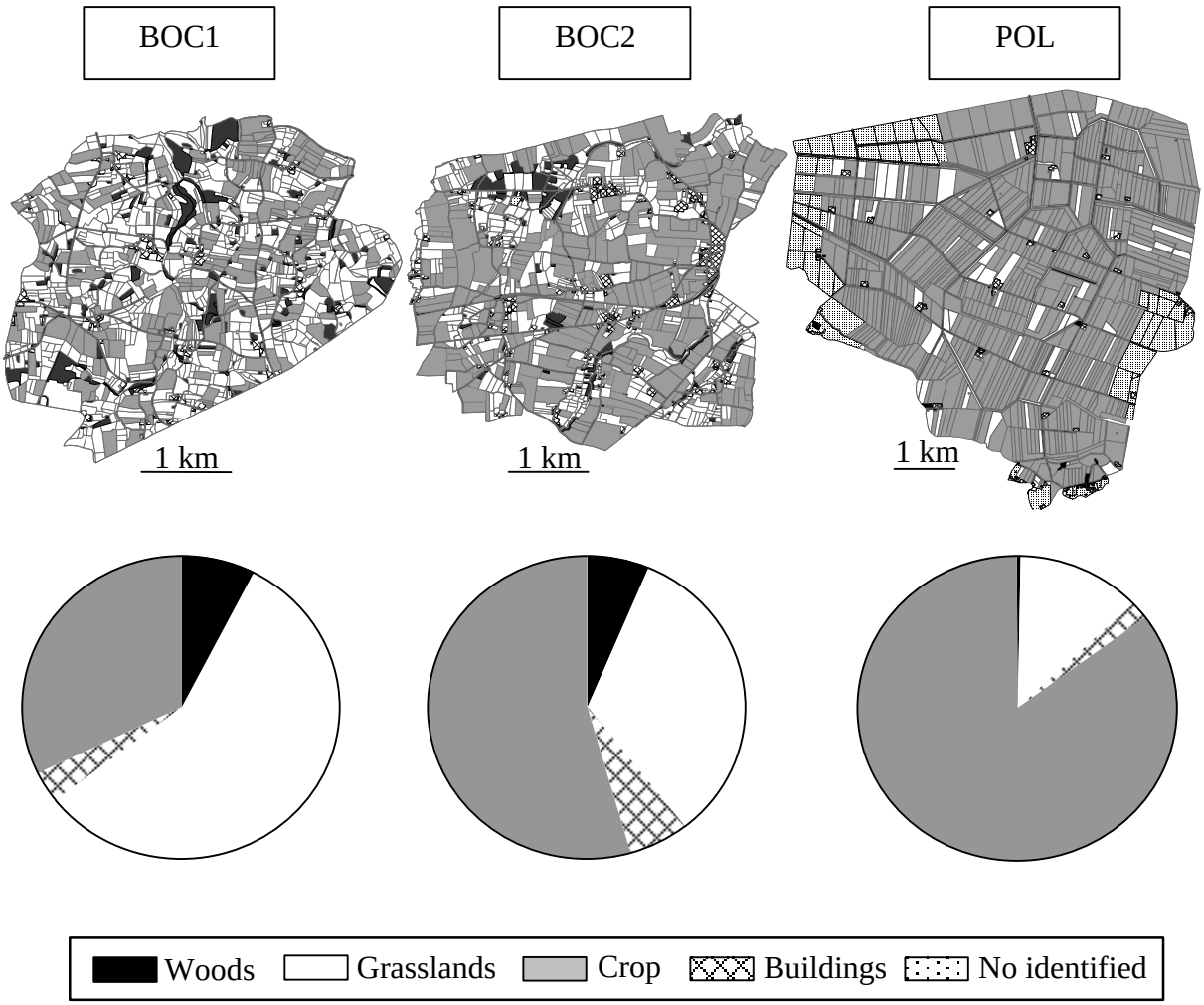

Figure 4.1.

Maps and proportions of the different land-cover in the three landscape units.

2) Data collection:

The study focused on the two most abundant diurnal raptor species in the region, the Common buzzard, *Buteo buteo*, and the Eurasian Kestrel, *Falco tinnunculus*. In order to sample raptor abundances in the three sites, we carried out a survey with several observation points corresponding to sampling units (10 observation points in BOC1, named A01 to A10; 9 observation points in BOC2, named C01 to C09, and 7 observation points in POL, named D01 to D07). In each sampling unit, five minutes of observations were made, using pairs of binoculars. We assumed a detection distance of 200-500m (Fornasari et al.1995 IN262). We made 12 observation sessions (one each month from November 2004 to October 2005). For

each raptor species, we used the annual cumulative individual numbers in each of the 26 observation points as an index of abundance. Maps of the sites with cumulative abundances in the observation points are given Appendix 6. For each site (BOC1, BOC2 and POL), we then calculated the average abundance of the Common buzzard and the Eurasian kestrel (average abundance of the 10 observation points in BOC1, of the 9 ones in BOC2, and of the 7 ones in POL). We also linked cumulative abundance in each of the 26 observation points to their landscape composition.

In the three sites, we extracted proportions of the different land-use (crops, woods, grasslands and buildings), and the length of hedgerows in a radius of 500 m around each of the 26 observation points (using geographical information system), in order to link raptor abundances with particular landscape elements in these windows.

A survey on the main prey abundance (small mammals) was also made in the three landscape units, for obtaining an estimation of the small mammal biomass available for predators. In this survey we only consider hedgerows for trapping small mammals, because it represents the main habitat for the majority of small mammal species in farming landscapes. However, this sampling method excludes other habitats such as grassland were some vole species could be numerous. Twenty four hedgerows were sampled using a standard trapping technique for seven trapping sessions (see Michel et al. (in press) for a more detailed trapping protocol (Chapters 1 et 2)). Individuals captured were weighted, giving a local relative biomass availability. By weighting this local relative biomass of small mammals by the hedgerow network densities at the three sites, we made an extrapolation to obtain small mammal biomass availability at the landscape level (g/ha) (see Chapter 1).

2) Data analysis:

We performed a principal component analysis (PCA) on the environmental data (land-use (ArcSin vX transformed) and hedge length) in a radius of 500 m around each observation point. We used ADE-4 software™ (Thioulouse and al. 1997). We extracted the coordinates of the 26 observation points on the first principal component axis of this PCA (accounting for 60% of the total inertia). We then link these coordinates to raptor abundances (log-transformed), using Minitab ™ software to test the linear regression.

A co-inertia analysis was performed using ADE-4 software ™ (Thioulouse and al. 1997) to relate the PCA on the matrix of environmental variables (26 sites x 6 variables) to the PCA on species abundances (26 sites x 2 species) (Dolédec and Chessel 1994). Co-inertia analysis is a two-table ordination method based on a covariance matrix (species x environment). It performs a simultaneous projection in the common scale of the two previous analyses onto a same co-inertia factorial plane. Species-landscape variables relationship was measured by the RV coefficient, which fluctuates between 0 and 100% (100% when the correlation between the two tables is total). A Monte–Carlo permutation test was performed to test if the percentage of covariation between the two tables (species and environment) was significant (number of permutations: 999). Detailed steps of co-inertia analysis are fully described in Dolédec et al. (1997).

Results

A total of 349 individuals were observed during the 12 observation sessions. 151 were Common buzzards, and 198 were Eurasian kestrels.

The average abundance of the two raptor species, the Common buzzard and the Eurasian kestrel (separated and combined), in the three sites are provided in Fig. 4.2A. The abundance of the Common buzzard shows a decline across the gradient of agricultural intensity (-81% from BOC1 to POL). The Mann-Whitney tests show that the Common buzzard abundance is significantly higher in BOC1 than in BOC2, and it is significantly smaller in POL than in BOC1 and BOC2 (Table 4.1). The abundance of the Eurasian kestrel also shows a tendency to decline from BOC1 to BOC2 and to POL (Fig. 4.2A), but this tendency is not significant (-40% from BOC1 to POL), whatever the sites considered (Table 1). Finally, considering both combined raptor species, abundance show a significant decline from BOC1 to BOC2 and from BOC2 to POL (Fig. 4.2A; Table 1) (-59% from BOC1 to POL). Small mammal availability was estimated in the three sites (Fig. 4.2B): the results follow a similar pattern of decline (-79% from BOC1 to POL) with the gradient of agricultural intensity (BOC1 > BOC2 > POL).

Table 4.1.
Comparison of raptor abundances in the three landscape units using the non parametric Mann-Whitney test.

Degree of significance :
n.s. = non significant
* = $p<0.05$
** = $p<0.01$

	BOC1			BOC2		
	W	*p*-value	Signif.	W	*p*-value	Signif.
Common Buzzard						
BOC2	126	0.036	*	/	/	/
POL	133	< 0.001	***	106	0.018	*
Eurasian Kestrel						
BOC2	111.5	0.370	n.s.			
POL	114	0.100	n.s.	92	0.312	n.s.
Buzzard + Kestrel						
BOC2	128	0.025	*	/	/	/
POL	131	0.002	**	102.5	0.043	*

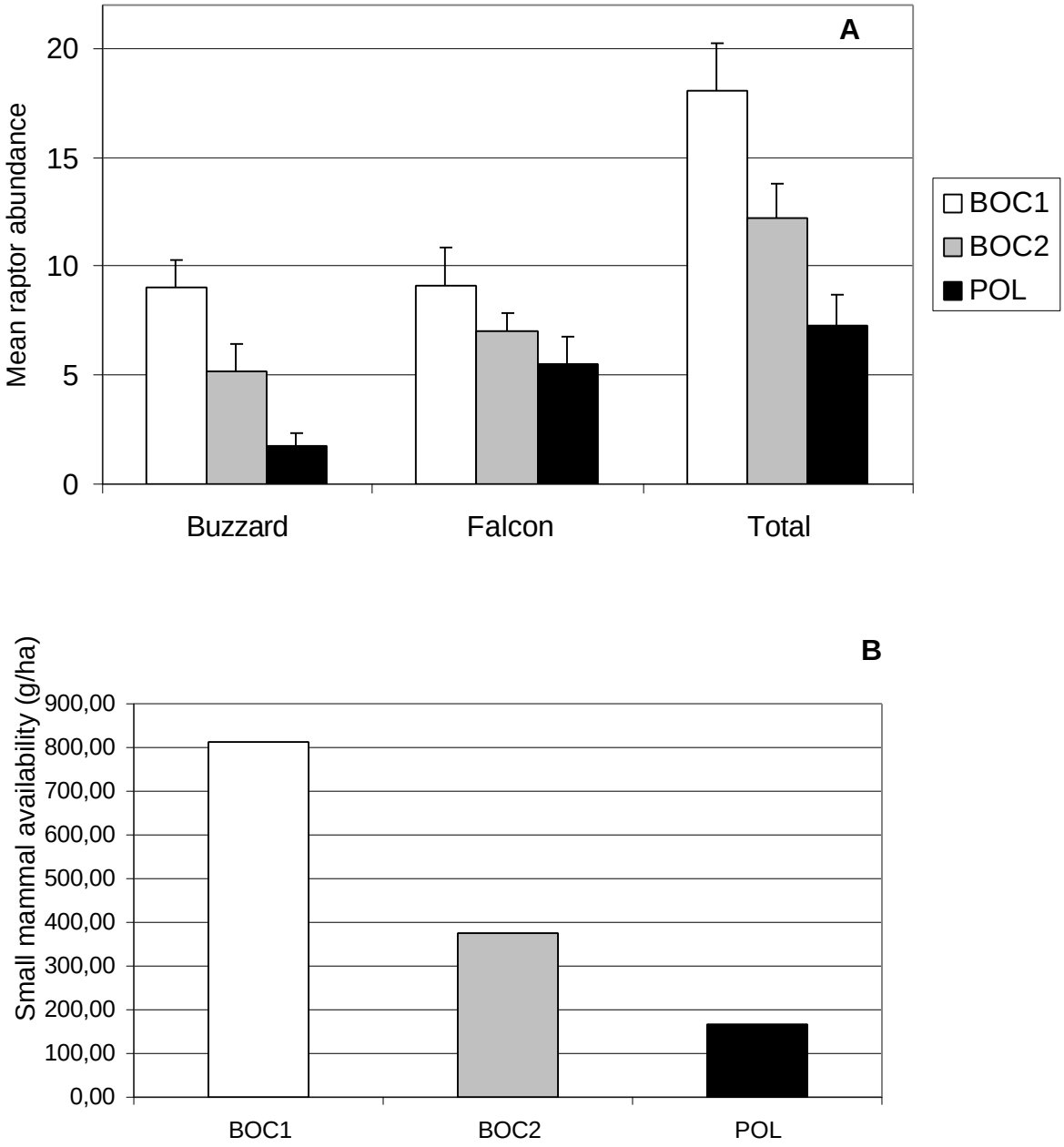

Figure 4.2.
(A) Mean abundances of buzzards and falcons (± sd) (separated and combined), and (B) small mammal availability in hedgerows (g/ha) in the three landscape units.

The results of the PCA analysis on the environmental data (land-use and hedge length) around each observation point shows a clear opposition among the sampling units of the three sites. The first principal component of this PCA performed on landscape characteristics

account for 60% of total inertia. On this axis, the sampling points of the BOC1 site (characterized by high proportions of semi-natural grasslands and woods, and high lengths of hedgerows) and the sampling points of the POL site (mainly characterized by crop fields), are totally opposed, while BOC2 site is in intermediate position. This first Principal Component axis correspond to a gradient of agricultural intensity in the sampling units (increase of the proportion of crops to the detriment of semi-natural grasslands, woods, and hedgerows). The results of the regression of the raptor abundances by the coordinates of the twenty six sampling units on the first Principal Component axis are given Fig. 4.3. The abundance of the Common buzzard responds significantly and negatively to the gradient of agricultural intensity (R^2adj. = 0.49; $p<0.001$) whereas the relation is not significant for the Eurasian kestrel (R^2 adj. = 0.07; $p = 0.10$).

Co-inertia analysis (Fig. 4.4) matches simultaneous positions of the 26 sampling units derived from covariance of the PCA on environmental data and PCA on species data (Fig. 4.4A). Projections of environmental variables and species are plotted onto the same co-inertia plane (Fig. 4.4B) and can be used to assess ecological gradients associated to co-inertia axes.

As shown by Monte-Carlo simulations, the co-inertia analysis was highly significant (RV = 47.8 %; $p<0.001$). The first axis accounted for 98% of co-inertia and the second axis for only 2%. When projected on the first co-inertia plane, the position of the sampling units, described by their environmental characteristics (circles), are close to their projection derived from their raptor composition (arrows) (Fig. 4.4A), showing a close link between landscape composition and raptor abundances. Nevertheless, we can note that some observation points are more discordant (e.g. A03, C02, D05, D07), showing in these cases, that raptor abundances are not in accordance with landscape composition in the observation points. For example, the observation point C02 exhibits raptor abundances closer to POL than to BOC2, with no Common buzzard observed. On the contrary, D05 is the POL sampling unit were Common Buzzards are the more abundant, which gives to D05 a position closer to BOC2. On a general point of view, observation points of the three sites are well separated on the first co-inertia axis, following the gradient of agricultural intensity. In the projection of raptor species and environmental variables, both the Common buzzard and the Eurasian kestrel are opposed to high proportion of crops. The buzzard is clearly associated with woods and hedgerows, indicating a possible greater dependence on small mammal availability, whereas the Kestrel is more associated with a high proportion of grasslands and seems to be less dependent to hedgerow small mammals.

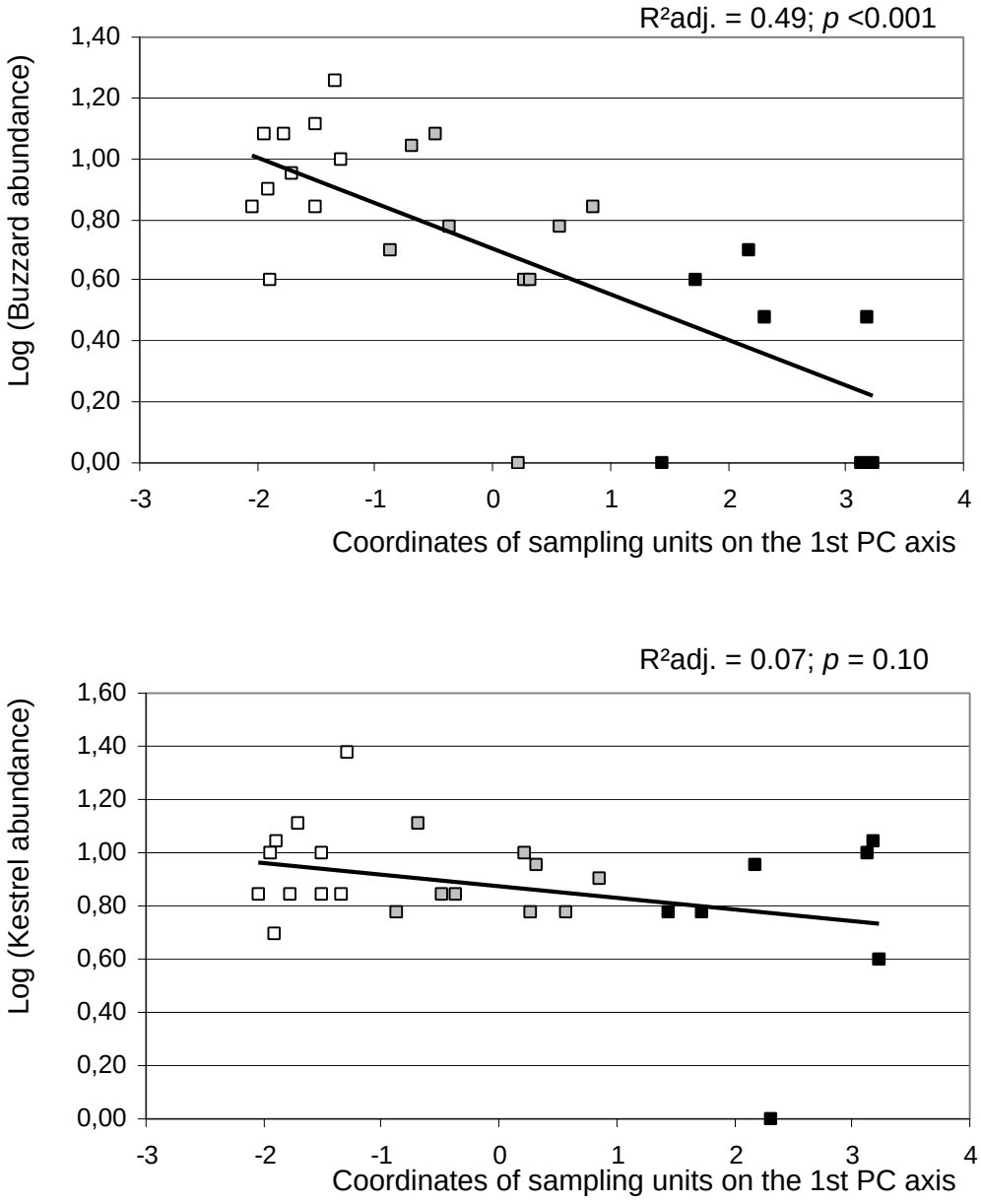

Fig. 4.3
Relationship between abundance of species in the sampling units and the coordinates of sampling units on the first axis of the land-cover PCA.

Observation points : □ BOC1 ▒ BOC2 ■ POL

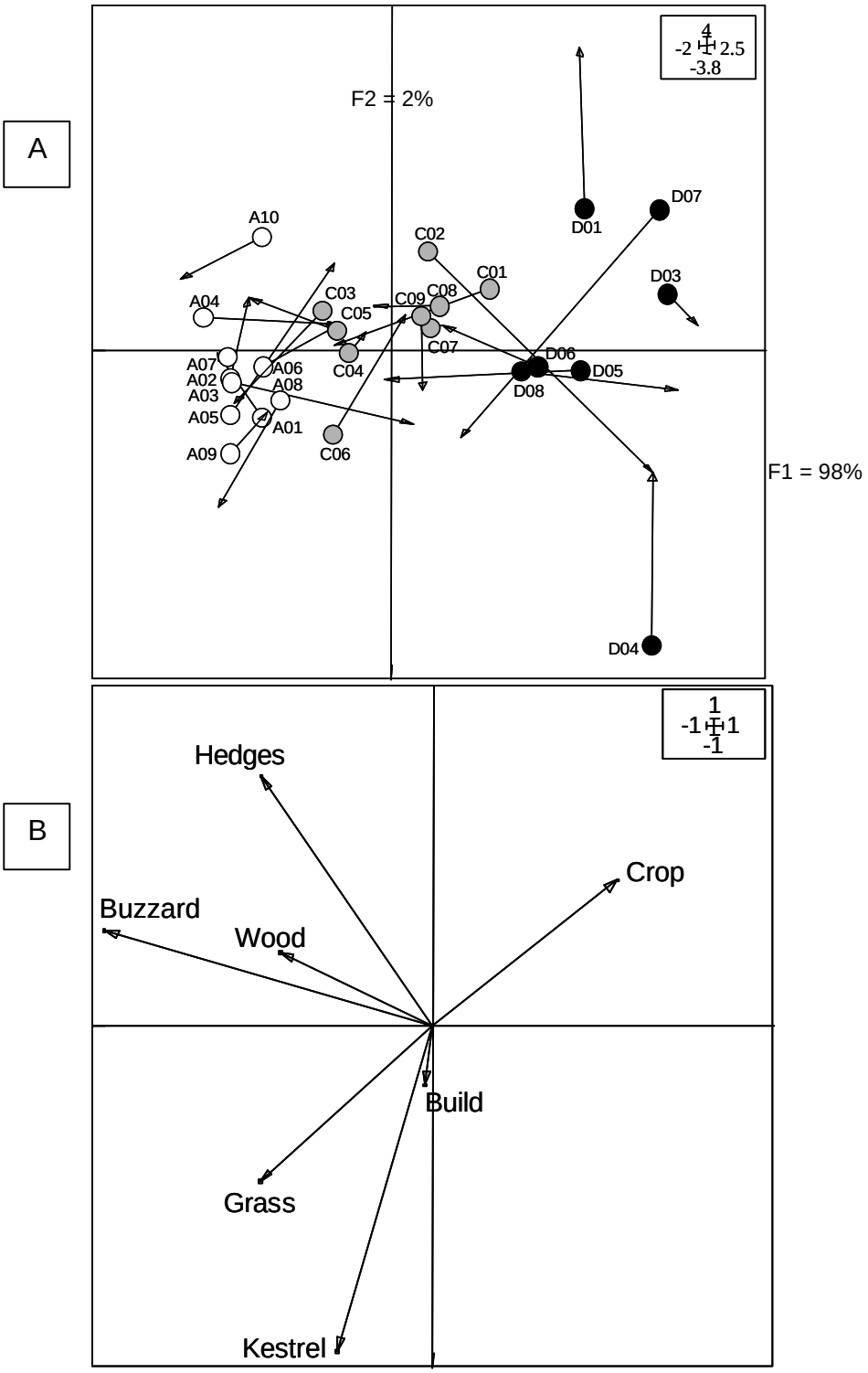

Fig. 4.4.

A. Graphical interpretation (factorial map of sampling units projection) of the co-inertia analysis of landscape and faunal data. Inertia explained by the two factorial axes is provided. Position of sampling sites (A01 to A10 = sampling units of BOC1; C01 to C09 = sampling units of BOC2; D01 to D08 = sampling units of POL (D02 was excluded of the analysis)), according to the landscape variables, are shown by their labels, and by circles (white for BOC1, grey for BOC2 and black for POL); arrows indicate positions of the same sampling sites according to the raptor abundances. The length of the segments is related to the difference between the two types of data for each site.

B. Projection of raptor species and landscape variables on the co-inertia plane.

Discussion

Our study reveals that abundances of two species of raptors, the Common buzzard and the Eurasian kestrel, respond differently toward agricultural intensification among three study sites. Those two species are widely distributed throughout Europe, but have exhibited a severe decline for several decades, coinciding with the period of European agricultural intensification that have dramatically affected the carrying capacity of most birds associated with these farmlands (Tucker and Heath, 1994, Pain and Pienkowski, 1997). Thanks to the use of the agricultural gradient along our three study sites, we can model the response of raptor abundance in front of agricultural intensification: it appears clearly that the landscape unit BOC1 (which is the site were hedgerows, woods, and grasslands are the more preserved), hosts the highest abundance of raptors, particularly for Common Buzzards. On the opposite, POL, which is the site where crops account for more than 90% of total area and where the hedgerow network is the most reduced, hosts the smallest abundance of Buzzard. BOC2 is intermediate both for agricultural intensity and Buzzard abundance. In front of a decreasing hedgerow density (-85%), and a decreasing proportion of grasslands (-71%) between BOC1 and POL, the abundance of the Common buzzard falls by 81% between the two opposite sites. The polders seems to have a too low proportion of woody habitats, limiting the presence of the Common buzzard. The significant response of this species is not similar for the Eurasian kestrel, from which the abundance only shows a tendency (abundance falling by 40% between BOC1 and POL), but is not significantly influenced by agricultural intensity.

How the spatial configuration of habitats affects the distribution and abundance of organisms is a question increasingly associated with landscape ecology (Flather and Sauer, 1996). But most studies concerning habitat use by raptors focus on “microhabitat” variables such as tree characteristics, ground cover or perches, often measured at small detailed scales (Fuller, 1979; Andrew and Mosher, 1982; Cody, 1985; Verner et al., 1986). This study was focused on the landscape scale, at which habitat fragmentation make sense. In fact, habitat fragmentation is a topic related to habitat selection that has been central in conservation biology and landscape ecology (Wicove, 1985; McGarigal and McComb, 1995). Fragmentation of wintering and breeding habitats for birds has been extensive and still occurs at fast rate across many areas (Richards, 1990; Skole and Tucker, 1993; Hansen et al., 2002) with negative demographic implications (e.g., Terborgh, 1989; Saunder et al., 1991; Robinson

et al., 1995; Donovan et al., 1997; Askins, 2000; Boulinier et al., 2001), as confirmed by our study. Reduction in the area of suitable habitat, such as, in the case of the Common Buzzard and the Eurasian Kestrel, woods and hedgerows for nesting and perching, and grasslands for foraging, can result in population declines by simply reducing adequate space for territories, nest sites, and other critical resources such as food availability (Rolstad, 1991). In our study, the Common Buzzard select habitat with high proportion of woods and hedgerows (the presence of woods is necessary in the habitat selection by Buzzards (Suetens, 1989)), whereas the Eurasian Kestrel show a preference for grasslands as confirmed by Suetens (1989).

The position of raptors at the top of food chains make them good indicators of ecosystem functioning (Newton, 1979). They show a tendency to forage in habitats attractive to small mammals (Thirgood et al. 2003). In our landscapes, hedges represent the permanent habitat for most of small mammal species. Consequently, in addition to the response to landscape characteristics, raptors might be expected to respond numerically to fluctuations in prey abundance and numerous long-term studies have documented this fact (Craighead and Craighead, 1956; Mindell et al., 1987; Korpimaki and Norrdahl, 1989, 1991; Village, 1990; Taylor, 1994; Potapov, 1997; Salamolard et al., 2000). In the present study, abundance of the Common Buzzard seems to be linked to small mammal availability in hedgerows at the landscape scale. But, as this small mammal availability is itself correlated to the hedgerow density, it is quite difficult to identify clearly the respective effects of the food versus habitat resources. Moreover, in our study, the prey availability is only based on trapping which was restricted to hedgerows. For obtaining a more valuable estimation of prey biomass really available at the landscape scale, it should be necessary to make an extensive trapping effort in the three sites, considering not only the hedgerow networks but also grasslands that could host higher abundances of some Microtine and shrew species, more vulnerable to avian predators that specialist species of hedgerows.

To conclude, we can say that agricultural intensification leads to responses which were different as a function of the target species considered. The Common Buzzard, more dependant to woody habitats, seems to be more vulnerable to agricultural intensification than the Eurasian Kestrel, more dependant to open habitats such as grasslands. As a conservation point of view, it should be essential to conserve semi-natural habitats (hedgerows, grasslands) in agricultural landscapes, for preserving these protected species.

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SYNTHESE ET DISCUSSION

SYNTHESE ET DISCUSSION

L'objectif de cette thèse était de contribuer à une meilleure compréhension des **patrons spatio-temporels** d'abondance et de diversité des petits mammifères dans les réseaux de haies des paysages agricoles.

Ce travail s'est intégré dans les problématiques de recherche communes à l'UMR 6553 ECOBIO et à l'INRA SAD de Rennes, réunies autour du site atelier de Pleine-Fougères de la Zone Atelier « Bretagne Continentale », sur les relations entre agriculture et biodiversité. Il fait également partie intégrante du programme « ECCO » (ECOSPHERE CONTINENTALE : Processus et Modélisation : « Fonctionnement et Dynamique de la Biosphère Continentale : processus, échanges de matières et d'énergie, modélisation [PNBC] »), sur le projet « Dynamique des paysages et flux trophiques : effets de la qualité des habitats et des paysages sur la disponibilité des proies (petits Mammifères) et l'abondance des prédateurs (rapaces) » porté par l'équipe Ecologie du Paysage de l'UMR ECOBIO.

Les principaux axes de recherche posés au préalable à ce travail étaient les suivants :

1) Quantifier la réponse de la communauté de petits mammifères, en terme de richesse, de diversité, d'abondance et de biomasse, dans des paysages agricoles contrastés, ayant des origines différentes et marqués par des différences de surfaces agricoles cultivées et de densité des réseaux de haies.
2) Identifier et hiérarchiser les variables environnementales responsables de la structure et de la composition de la communauté, dans une approche pluri-échelle, de la station d'échantillonnage à l'unité paysagère.

3) Faire émerger des patrons temporels de l'abondance de la communauté et des populations de petits mammifères qui la composent, en réponse à la composition et à la dynamique des paysages.

4) Estimer l'effet du paysage et de la disponibilité en proies (les petits Mammifères) sur un niveau trophique supérieur, avec l'exemple de l'abondance de deux rapaces diurnes, la buse variable (*Buteo buteo*) et le faucon crécerelle (*Falco tinnunculus*).

Dans cette discussion je ferai une synthèse des points forts obtenus par rapport à ces objectifs, en appuyant sur les apports de ce travail par rapport aux études antérieures menées dans les mêmes sites, en en soulignant les limites, et en proposant de nouvelles perspectives de recherche.

Pour étudier la réponse des communautés à l'intensification de l'agriculture, la méthode la plus rigoureuse serait de mener une étude à long terme pour mettre en relation une évolution des caractéristiques des espèces étudiées (richesse spécifique, diversité, abondance…) avec l'évolution temporelle des pratiques agricoles qui influencent la diversité et la composition des paysages ruraux. De telles études, très lourdes à entreprendre, ont été regroupées dans les synthèses de Stoate et al. (2001) et de Robinson et Sutherland (2002), montrant clairement une perte de biodiversité qui a accompagné l'intensification de l'agriculture au cours des dernières décennies. Dans la plupart des cas, ce n'est pas le nombre d'espèces qui est touché, mais les fréquences de ces espèces, qui tendent à se raréfier, pour de nombreux taxons, plantes, invertébrés ou vertébrés.

Nous avons initié, par le programme ECCO, une étude sur le long terme avec le projet sur l'abondance des rapaces dans le site Atelier de Pleine-Fougères, qui est amené à se poursuivre plusieurs années. Mais mettre en place de telles études sur le long terme est difficile. Dans le cadre temporel limité de la thèse, l'utilisation d'unités paysagères présentant des niveaux d'intensité de l'agriculture contrastés et des caractéristiques paysagères qui en découlent différentes, le long d'un gradient, a été la solution la plus parcimonieuse pour une étude de la réponse de la biodiversité à l'évolution de l'agriculture. Le site atelier de Pleine-Fougères offre en effet la possibilité de travailler sur trois unités paysagères bien distinctes, qui pourraient mimer l'intensification temporelle de l'agriculture, d'un système peu intensifié

d'élevage de bovins, caractérisé par une dominance prairiale et un réseau de haies dense, à un système de cultures intensives à plus de 90%. Les trois sites peuvent être ordonnés de la façon suivante : BOC1 < BOC2 < POL, d'après les changements paysagers observés : augmentation des surfaces cultivées au détriment des prairies, augmentation de la taille des parcelles accompagnée de la réduction du linéaire de haies qui se traduit par une augmentation du grain paysager. De plus, les sites bocagers sont à opposer aux polders par le fait même de leur histoire très différente d'un site néoformé.

Caractérisation de la structure et de la composition de la communauté de petits mammifères en réponse aux paysages contrastés :

Dans ce contexte, la caractérisation de la communauté de petits Mammifères des haies a été faite à l'aide d'indices synthétiques de mesures de la diversité biologique (la richesse spécifique et l'indice de diversité de Shannon), ainsi que de mesures d'abondances et de biomasses des différentes espèces composant la communauté.

La richesse spécifique est apparue comme étant un mauvais indicateur de la réponse de la communauté à l'intensification de l'agriculture. En effet, les trois unités paysagères présentent des richesse spécifiques tout à fait comparables : huit espèces pour les sites BOC1 et BOC2 (Mulot sylvestre, Campagnol roussâtre, Campagnol souterrain et Campagnol agreste pour les espèces de rongeurs, et musaraignes musette, couronnée, pygmée et aquatique pour les espèces d'insectivores). Seule la musaraigne aquatique est absente du site POL, qui compte un total de sept espèces capturées. Mais cette différence a été jugée non significative car un seul individu a été capturé dans BOC1 et deux individus dans BOC2. Ce faible taux de capture pour la musaraigne aquatique est du à la rareté de cette espèce, protégée en France, et qui nécessite des habitats particulièrement préservés et humides. Une étude préalable (Paillat, 2000 ; Burel et al. 2004), menée sur le même gradient paysager, mais avec la méthode indirecte d'analyse des pelotes de réjection des chouettes effraye (*Tyto alba*), a abouti à des résultats similaires avec égalité de la richesse spécifique dans les différents sites, toutefois supérieure à celle obtenue par piégeage en raison de la limitation de notre échantillonnage aux seules haies (voir Annexe A pour article sur la comparaison des méthodes). Il est possible que

des extinctions locales puissent avoir lieu pour certaines espèces de petits mammifères, mais rarement à l'échelle d'un paysage tout entier (Merriam et Wegner, 1992), d'autant plus pour les espèces généralistes et mobiles telles que le mulot sylvestre, qui peut se déplacer à travers une large gamme d'habitats au sein de la matrice agricole. Dans le cas d'espèces très spécialistes, inféodées à un type particulier d'habitat, tel que l'habitat boisé (haies, bosquets, bois) pour le campagnol roussâtre, des extinctions peuvent se produire dans des fragments très isolés (Geuse et al., 1985 ; Apeldoorn et al., 1992 ; Paillat et Butet, 1996), mais ces espèces ont généralement de fortes potentialités de recolonisation et peuvent donc également se maintenir à l'échelle du paysage (Szacki et Liro, 1991 ; Ylonen et al., 1991 ; Kozakiewicz et al., 1993), conférant à la communauté une forte robustesse.

En revanche, la représentation des différentes espèces composant le peuplement varie en fonction du paysage : l'indice de diversité de Shannon a permis de discriminer clairement les sites, en mettant en évidence une forte opposition entre d'un coté les deux sites de bocages, BOC1 et BOC2, qui présentent une diversité très semblable, et de l'autre coté le site POL, dont les haies ont une diversité plus faible. Le peuplement est donc plus équilibré dans les haies des bocages, les sites les moins intensifiés. La baisse de diversité observée avec l'intensification de l'agriculture est une constante dans de nombreuses études de mise en relation de la biodiversité et de l'agriculture, et ce, pour de nombreux taxons, plantes (Andreasen et al. 1996 ; Donald, 1998), invertébrés (Warren et Kirkland, 1997), oiseaux (Tucker et Heath, 1994) ou mammifères (Harris et al., 1995). On peut remarquer que cette perte de diversité ne suit cependant pas de manière linéaire le gradient d'intensification agricole tel qu'il a été défini (proportion de la surface en culture ; densité du réseau de haies) puisque les deux sites bocagers, bien que contrastés du point de vue de l'agriculture et de la structure paysagère, présentent des diversités non significativement différentes. L'origine commune de ces deux paysages bocagers, bien différente de celle des polders, peut sans doute expliquer cette ressemblance de diversité.

L'abondance de la communauté, ainsi que les abondances des espèces qui la composent sont également très semblables entre les deux sites BOC1 et BOC2. Les valeurs d'abondance totale de la communauté suivent un profil inverse à celui observé pour les valeurs de diversité puisque ce sont les haies échantillonnées dans le site le plus intensifié (POL) qui hébergent les abondances de petits mammifères les plus importantes. Et il en est de même pour les valeurs de biomasses : les haies des polders sont potentiellement plus riches en biomasse disponible pour les prédateurs que les haies des bocages. Mais ce résultat a une

valeur de disponibilité locale, et pour obtenir une valeur de disponibilité en proies dans les haies à l'échelle du paysage, les valeurs de biomasses locales doivent bien évidemment être pondérées par le linéaire total de haie (dans une étude future il conviendrait cependant de vérifier la représentativité de ces haies par rapport au réseau de manière à être sur de la validité de cette extrapolation). Dans ce cas, la biomasse paysagère des petits mammifères dans les haies suit de manière linéaire le gradient d'intensification de l'agriculture : BOC1 > BOC2 > POL. Ce résultat sera discuté dans le cadre de la fonction de proie des petits mammifères.

Facteurs de la structuration spatiale de la communauté de petits mammifères :

Leur origine, très différente, ainsi que la diversité des systèmes de production ont créé une diversité de paysages ordonnées le long d'un gradient d'intensification agricole, marqué par la réduction des réseaux de haies et de la proportion des prairies, et par l'augmentation des surfaces cultivées et du grain paysager. Il a été montré dans de nombreuses études que la configuration du paysage est un facteur qui peut avoir une forte influence sur les assemblages d'espèces de petits mammifères (Hansson, 1977 ; Barrett et Peles, 1999 ; Bowman et al., 2001 ; Raoul et al., 2001 ; Martin et McComb, 2002). Dans notre étude, le paysage est clairement un facteur fort de la structuration de la communauté, mettant en exergue l'opposition entre le site des polders, largement dominé par deux espèces, le mulot et le campagnol roussâtre, et les sites de bocage dans lesquels les espèces les moins abondantes sont plus amplement représentées.

Mais de manière plus fine, l'abondance des espèces composant la communauté va être influencée par des éléments particuliers composant le paysage. C'est particulièrement vrai pour les espèces de musaraigne : les musaraignes couronnée (*Sorex coronatus*) et pygmée (*Sorex minutus*) se rencontrent en plus forte densité dans les haies entourées de fortes proportions de prairies et de bois et d'un réseau de haies dense. Ces deux espèces sont en effet connues pour être associées et dépendantes d'habitats préservés et de paysages richement boisés (Lovari et al., 1976 ; Böhme, 1978 ; Taberlet, 1986 ; Hutterer, 1990). Ces éléments du paysage peu perturbés reçoivent en effet beaucoup moins d'intrants chimiques que les

éléments cultivés, ce qui se répercute sur les bords de champs, donc les haies, moins soumis aux pesticides, permettant d'héberger des ressources en invertébrés plus optimales pour les musaraignes. Il est a noter que Love et al. (2000) trouvaient un résultat contradictoire pour la musaraigne pygmée, puisque son abondance augmentait dans le régime alimentaire de la chouette effraye avec l'intensification de l'agriculture. La musaraigne musette quand à elle est une espèce connue pour être beaucoup plus tolérante vis-à-vis de l'intensification de l'agriculture (Millan de la Pena et al., 2003), ce qui explique son association avec des haies entourées de grandes proportions de maïs, qu'elle peut exploiter pour sa recherche de nourriture lorsque le couvert est suffisant (Genoud et Hutterer, 1990).

Cette influence des éléments du paysage n'a pas été mise en évidence pour toutes les espèces, particulièrement pour le mulot (*Apodemus sylvaticus*), qui est l'espèce dominante dans les trois sites, même si son abondance est supérieure dans les haies des polders par rapport aux haies des bocages. Le fait de ne pas avoir détecté d'éléments du paysage pouvant influencer l'abondance du mulot est à relier à sa nature ubiquiste et eurytopique (Orsini, 1981 ; Butet, 1984 ; Canova et Fasola, 1991). C'est en effet, au sein de la communauté, l'espèce la plus généraliste et la plus mobile, capable d'exploiter une large gamme d'habitats. Love et al. (2000) ont même mis en évidence une augmentation de la fréquence du mulot dans le régime alimentaire de la chouette effraye, parallèlement à l'intensification de l'agriculture en Grande-Bretagne.

Mais nous avons mis en évidence que le paysage n'est pas le seul facteur explicatif des assemblages d'espèces. En effet, les différences entre les haies sont plus importantes que les différences entre les sites, ce qui laisse présager de l'influence de facteurs locaux. La structure et la composition de la communauté sont en effet contrôlées à l'échelle plus fine des stations de piégeage : les caractéristiques intrinsèques des éléments, donc de l'habitat, jouant notamment un rôle très important dans l'abondance du campagnol roussâtre, *Clethrionomys glareolus*. En effet, des haies présentant une grande largeur et une forte richesse en éléments arborés sont très favorables à la présence et à l'abondance de cette espèce. Cela peut s'expliquer par la spécificité d'habitat du campagnol roussâtre, connu pour être très inféodé au milieux boisés ou aux haies dans les paysages agricoles. Le caractère très forestier de certaines haies, particulièrement les haies des polders est donc très favorable à cette espèce.

On peut donner également l'exemple d'une espèce beaucoup plus minoritaire, le campagnol souterrain (*Microtus subterraneus*), dont l'abondance peut aussi être reliée à des

caractéristiques d'habitat puisque elle est corrélée à la richesse spécifique en herbacées des haies. Cette espèce est en effet plus communément rencontrée dans les milieux prairiaux que dans les milieux boisés compte tenu de son caractère herbivore, et elle trouvera donc un niveau de ressource supérieur dans les haies présentant une riche strate herbeuse.

Pour conclure, il est important de noter que les patrons d'abondance de la communauté à l'échelle du paysage sont accentuées par une intégration des phénomènes qui se déroulent à une échelle plus fine. Les effets paysagers se répercutent de façon cohérente à l'échelle de l'habitat : les espèces défavorisées par l'intensification agricole à l'échelle du paysage sont encore plus dominées par les espèces plus résistantes, qui deviennent, comme le campagnol roussâtre, encore plus dominante par le fait des facteurs locaux. C'est donc bien l'intégration des phénomènes à différentes échelles qui structure la communauté de petits mammifères. C'est un point fort de cette étude par rapport aux études antérieures menées sur les petits mammifères dans les mêmes sites (Paillat, 2000) ou sur un autre gradient agricole en Bretagne (Millan de la Pena et al., 2003), qui étaient restreintes à l'échelle du paysage, du fait même du protocole utilisé (analyse des pelotes de réjection des chouettes effrayes). Notre étude confirme les résultats obtenus au préalable avec cette méthode, et permettent d'intégrer l'échelle et l'influence de l'habitat sur les assemblages d'espèces.

Dynamique temporelle de la communauté de petits mammifères :

Nous avions émis l'hypothèse que compte tenu de l'influence du paysage sur la structuration spatiale de la communauté, l'appartenance à une unité paysagère donnée pouvaient aussi avoir des répercutions sur la structuration temporelle des assemblages d'espèces, en raison de la dynamique différente des trois paysages (nombres de labours et d'interventions dans les parcelles plus nombreux dans le site le plus intensifié). Cette hypothèse ne s'est pas vérifiée : la structure temporelle de la communauté dans les haies est la même, quelle que soit l'unité paysagère considérée, et au sein de chacun des sites quelles que soient les haies d'échantillonnage. Les différences entre les caractéristiques des trois sites n'ont donc pas d'effet sur les patrons temporels des espèces. En revanche, c'est l'intensité des variations saisonnières d'abondance de la communauté qui a été touchée : le site le moins

intensifié, BOC1, présente les fluctuations d'abondances les plus faibles au cours de l'année. Par contre, l'amplitude d'abondance est maximale dans le site des polders. Il apparaît donc qu'un système plus stable entraîne des fluctuations d'abondance de faible amplitude alors que dans un système plus dynamique, les variations saisonnières d'abondance sont beaucoup plus marquées. De plus, des études ont montré qu'une communauté plus diversifiée (c'est la cas des sites bocagers) était plus stable qu'une communauté simplifiée (forte dominance de deux espèces comme dans les polders) (Salamolard et al., 2000), ce qui pourrait également expliquer les fortes variations d'amplitude dans les haies des polders.

Ces grandes amplitudes de fluctuations dans l'abondance totale de la communauté sont surtout le fait des deux espèces dominante dans le peuplement, et en premier lieu le mulot. *Apodemus sylvaticus* présente des variations saisonnières caractéristiques de cette espèce, avec une abondance très faible en été, et beaucoup plus forte au printemps, et surtout à l'automne. C'est un profil qui a été mis en évidence par de nombreux auteurs, dans différents types d'habitats, et tout particulièrement dans les haies des paysages agricoles (Montgomery et Dowie, 1993; Butet, 1994 ; Rogers et Gorman, 1995; Kotzageorgis et Mason, 1997). On a d'ailleurs montré dans notre étude que c'est un profil saisonnier qui se répète d'année en année, avec des données de captures qui présentent la même dynamique saisonnière en 1995, 2003 et 2004. Ce profil particulier est à mettre en relation avec le caractère ubiquiste du mulot, capable, comme on l'a vu plus haut, d'exploiter différents types d'habitats en fonction des possibilités de ressources qu'ils offrent. Ainsi, à la fin du printemps, lorsque les cultures ont atteint un couvert végétal suffisant, le mulot quitte les haies pour gagner les champs cultivés et les exploiter jusqu'à la récolte des cultures (Loman, 1991 ; Fitzigibbon, 1997 ; Ouin et al., 2000), au moment de laquelle les individus reviennent massivement dans les haies qui leur servent d'habitat permanent pendant les saisons automnales et hivernales, lorsque les champs adjacents sont mis à nu. Le mulot augment ainsi la surface de son territoire pour la reproduction, ce qui induit l'effet de masse automnal lors du retour dans les haies à une période où la territorialité ne s'exprime plus. Cela explique les fortes amplitudes de fluctuations observées dans le site POL, dont les haies sont entourées de cultures, potentielles ressources estivales. Par contre, on fait l'hypothèse que les prairies, très nombreuses, qui entourent les haies du site BOC1, ne fournissent pas un habitat de bonne qualité pour la dispersion estivale des individus, qui restent donc dans les haies où ils accomplissent leur cycle annuel, n'engendrant pas de grandes amplitudes de fluctuations saisonnières.

Les autres espèces, à l'exception de la musaraigne musette, sont plus strictement inféodées aux haies. Leurs effectifs croissent donc au cours de l'année de manière modérée, puisque leur espace de reproduction est plus restreint (les plus grandes amplitudes de variation étant observées pour le campagnol roussâtre, *C. glareolus*), et sont souvent les plus élevés en été et en automne, période à laquelle la diversité de Shannon de la communauté est maximale. Pour les musaraignes, une hypothèse de compétition inter-spécifique a été émise, en particulier pour expliquer la baisse d'abondance de *Sorex coronatus* et *S. minutus* lorsque *Crocidura russula* (de plus grande taille) voit ses effectifs augmenter à la fin de l'été (Hanski and Kaikusalo, 1989).

Effets du paysage et de la disponibilité en petits mammifères sur un niveau trophique supérieur :

Il était intéressant, en plus des données numériques sur les petits mammifères, d'avoir une estimation de l'impact des différences de composition du paysage dans nos trois sites sur un niveau trophique supérieur, ce qui nous a conduit à nous interroger sur l'aspect fonctionnel de cet communauté en nous intéressant à la fonction de « proies » des petits mammifères. L'étude des variations de régime alimentaire d'un rapace, prédateur du peuplement, comme la chouette effraye a déjà été menée (Annexe A, et voir Paillat 2000, et Millan de la Pena et al., 2003).

Nous avons choisi d'estimer l'abondance de deux espèces de rapaces diurnes, la buse variable (*Buteo buteo*) et le faucon crécerelle (*Falco tinnunculus*) en réponse à la composition des paysages, ainsi qu'au gradient de disponibilité en proies. A l'échelle de l'Europe, les effectifs de ces deux espèces ont fortement diminué au cours des dernières décennies (Tucker et Heath, 1994; Pain et Pienkowski, 1997), en lien direct avec l'intensification agricole européenne. Dans nos sites d'étude, il apparaît que la buse et le faucon répondent de manière différentes. Comme nous l'avions mis en évidence dans le chapitre 1, les biomasses de petits mammifères des haies disponibles à l'échelle du paysage sont maximales dans le site BOC1, intermédiaires dans le site BOC2, et les plus faibles dans le site POL (diminution d'un facteur 7 entre BOC1 et POL). L'abondance de la buse variable suit le même profil et décroît de manière significative avec la diminution de la biomasse disponible dans les haies (diminution d'un facteur 6.5 entre BOC1 et POL). L'abondance du faucon crécerelle montre une tendance

qui va dans le même sens (diminution d'un facteur 2.5) mais qui n'est pas significative. Il en est exactement de même pour la relation entre les abondances des rapaces et le gradient paysager : les effectifs observés de buses diminuent quand les éléments permanents diminuent au profit des cultures, alors que l'abondance du faucon crécerelle décroît modérément le long du gradient. L'approche à l'échelle des points d'observations a toutefois permis de montrer que les deux espèces de rapaces s'opposent à la présence de cultures. La buse est étroitement associée aux habitats boisés (bois et réseau de haies), indiquant peut-être une plus forte dépendance aux petits mammifères des haies. Ainsi il apparaît que le site des polders présente un taux de boisement limite pour l'accueil des buses. Le faucon crécerelle montre, quand à lui, une plus forte relation à la présence de prairie, indiquant sa moindre sensibilité à l'ouverture du paysage (Suetens, 1989). Il reste cependant difficile, en l'état actuel de l'étude, de distinguer les effets respectifs de la disponibilité en habitats et de celle en proies sur l'abondance de ces deux espèces de rapaces.

Agriculture et biodiversité : quels apports ?

Tout d'abord, dans notre contexte d'étude, se pose la question de savoir si on a bien à faire à un gradient d'intensification agricole. Dans le sens d'une augmentation des surfaces cultivées et d'une diminution des éléments semi-permanents (prairies, haies) c'est le cas. Mais l'intensification de l'agriculture dans son ensemble recouvre d'autres aspects que nous n'avons pas pris en compte, tels que la quantité d'intrants chimiques (fertilisants, pesticides), ou encore la qualité des sols et la qualité de l'eau (…). Plus qu'un véritable gradient d'intensification, on est face à des systèmes d'origines différentes, soulignant une opposition nette entre les bocages (plus ou moins intensifié) et les polders. L'utilisation d'un troisième site bocager plus intensifié que BOC2 pour former un **gradient bocager** de sites ayant la même origine serait donc intéressant, puisque peu de différences ont été mises en évidence entre BOC1 et BOC2.

Les publications récentes (Stoate et al., 2001 ; Robinson et Sutherland, 2002) fournissent les premières synthèses sur les réponses des communautés animales ou végétales en lien avec **l'homogénéisation** des paysages agricoles découlant de l'intensification de l'agriculture. Ces auteurs montrent que les communautés se simplifient (perte de diversité), mais sont souvent plus **instables** (amplitudes de fluctuations plus marquées), ce qui va dans le

même sens que ce que nous avons mis en évidence. De plus, comme nous l'avons montré, cette simplification est le plus souvent à l'avantage des espèces **généralistes** qui deviennent dominantes dans les peuplements. La perte des habitats favorables dans les paysages agricoles constatée depuis plusieurs décennies s'est en effet le plus souvent répercutée sur les espèces **spécialistes**, c'est-à-dire plus strictement inféodées à ces types d'habitats (haies, prairies, bois) que les espèces généralistes beaucoup plus ubiquistes et donc beaucoup moins sensibles. A l'échelle globale du paysage, Paillat (2000) et Millan de la Pena (2003) ont montré que le régime alimentaire de la chouette effraye, principalement composé de petits mammifères était différent entre des sites contrastés et allait dans ce sens (plus forte dominance des généralistes dans les sites offrant le moins d'habitat favorable), ce qui se retrouve à l'échelle des haies. Grâce à notre étude à cette échelle beaucoup plus locale, nous avons montré que les caractéristiques intrinsèques de l'habitat peuvent également jouer un rôle important, y compris pour les espèces spécialistes, en fournissant une qualité très favorable, même dans des paysages limitant au niveau de la quantité d'habitat. Ainsi, la prise en compte intégrée des **échelles locale et paysagère** paraît primordiale dans la description des patrons de biodiversité dans les paysages agricoles, les facteurs agissant sur les assemblages d'espèces intervenant à ces deux niveaux, supérieur (paysage), et inférieur (habitat).

Perspectives

1) Effet des pratiques agricoles locales sur la communauté de petits mammifères :

Nous avons mis en évidence que, en plus des caractéristiques paysagères, les caractéristiques intrinsèques des stations de piégeage avaient un rôle majeur dans la structuration de la communauté de petits mammifères. La qualité de l'habitat est donc un facteur important à prendre en considération. Mais au sein des paysages agricoles, les bords de champs, donc les haies sont en contact direct avec les parcelles adjacentes et les pratiques qui y sont menées, et sont eux-mêmes soumis à des modes de gestions différents. Il serait donc très intéressant pour quantifier la qualité d'un élément permanent de considérer les pratiques agricoles qu'il subit, directement ou indirectement. Ainsi la disponibilité en ressources pourrait être affecté par des passages répétés de pesticides en bordures de haies (ou directement dans l'élément) qui éliminerait la strate herbacée, ou d'insecticides qui affecterait la quantité d'invertébrés disponibles. Une collaboration avec l'INRA SAD de Rennes est en

cours afin de mettre en place un indice basé sur la présence d'un certain nombre d'espèces végétales dans les haies qui permettrait d'estimer le niveau de perturbation lié aux pratiques agricoles subit par les haies. Ainsi, en fonction des espèces présentes dans la strate herbacée, on pourrait attribuer un caractère adventice, prairial ou forestier à chaque haie, indicateur des perturbations reçues, que l'on pourrait mettre en lien avec les profils d'abondance de la communauté de petits mammifères dans ces haies.

2) Estimation de disponibilité paysagère de petits mammifères :

Dans le but d'estimer la biomasse relative disponible constituée par les petits mammifères à l'échelle du paysage, nous avons, dans notre étude considéré uniquement le réseau de haies, puisque le piégeage a été effectué dans cet habitat. De plus, l'extrapolation c'est faite à partir d'un nombre limité de haies (800 m par unité paysagère), pondéré par la densité du réseau. Pour ces raison, cette mesure de biomasse paysagère ne nous semble pas satisfaisante pour quantifier la disponibilité en petits mammifères pour les rapaces, qui ont accès au cours de leur recherche de nourriture à d'autres types d'habitats. Il conviendrait donc, à l'intérieur de chacune des zones d'observation des rapaces, de procéder à une estimation plus fine, et multi-habitat de l'abondance des proies, en échantillonnant dans un nombre plus important de haies, mais aussi, et surtout, dans d'autres habitats, tels que les prairies, les bandes herbeuses, les digues, et même les cultures.

Aménagement :

Une meilleure adéquation entre les objectifs de production et la nécessité de la conservation de la biodiversité dans les paysages agricoles se fait de plus en plus par les programmes agri-environnementaux, dans lesquels les agriculteurs sont payés pour modifier leurs pratiques. Ces programmes concernent à la fois l'aménagement des paysages et les opérations de gestion concernant les pratiques locales. Les mesures concernent principalement la restauration ou, plus souvent le maintien des éléments semi-permanents tels que les bois, mais surtout les haies et les prairies, zones refuges pour de très nombreuses espèces des milieux agricoles, et la diminution de l'utilisation des intrants chimiques (pesticides et

fertilisants) dans les mode de gestion des parcelles cultivées ou des éléments d'incultures adjacents.

Notre étude a permis de montrer que la composition du paysage est un élément majeur dans la structuration des communautés (ce qui a été montré également pour de nombreux autres taxons), et doit donc, en tant que tel, être intégré dans l'élaboration des mesures agri-environnementales de gestion et d'aménagement pour la conservation de la biodiversité. Dans les cas des paysages que nous avons étudié, les propositions d'orientations envisagées doivent contribuer à la quantité et la qualité des habitats refuges, qui doivent être des structures permettant le maintien d'unités démographiques stables et fonctionnelles. Ainsi, dans les paysages très ouverts, dans lesquels les proportions des éléments semi-permanents sont très faibles, la priorité devra être faite sur la restauration de ces habitats. Leur agencement devra bien évidemment être pris en compte, de manière a former dans le paysages une trame connectée d'habitats favorables, et non des patchs de grandes tailles mais complètement isolés. Dans ces paysages ouverts, mais également dans les paysages riches en éléments permanents denses et connectés, une attention particulière devra être portée sur la qualité des éléments, qui pourra être augmenté par un élargissement des bords de champs, permettant d'accueillir une biodiversité plus abondante, et en modifiant les pratiques de gestion effectuées par les agriculteurs.

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ANNEXES

Annexe A : Article :

Efficiency of trapping techniques versus Barn Owl pellets analysis for assessing changes in small mammal communities along landscape gradients.

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(soumis à ACTA THERIOLOGICA)

Barn Owl (*Tyto alba*)

Efficiency of trapping techniques versus Barn Owl pellets analysis for assessing changes in small mammal communities along landscape gradients.

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Running head : Small mammal trapping versus Barn Owl pellet analysis

Abstract

In this paper we estimated richness, diversity and abundance of small mammal species in three agricultural landscape contexts with two sampling techniques : trapping and Barn Owl pellet analysis. Our aim was to compare composition and structure of the small mammal community and to know which species may be used as good indicators of land use changes according to the sampling method used. A greater diversity of species was obtained when using pellet analysis instead of trapping and our study corroborates previous findings reporting that Barn Owls would tend to over sample shrews and open grassland rodent species whereas traps would over sample rodents from dense covered field boundary habitats. Nevertheless, comparison of these two techniques indicate that some small mammal species seems to be eaten by Barn Owl proportionally to their availability in its hunting area. When using Barn Owl pellet analysis, these prey species may become useful indicators for long term studies of land use changes occurring in agricultural landscape.

Key-words

Trapping, Barn Owl pellet analysis, Land use changes, small mammal; diversity

Introduction

Recent changes in agriculture are often pointed as the main causes that have led to a widespread decline in farmland biodiversity across many taxa (Robinson and Sutherland, 2002). The term « biodiversity » is relevant for a large range of life organization levels such as populations, communities, biocenosis and functional processes (Büchs, 2003). In order to evaluate consequences of land use changes on biodiversity, more and more researches are involved in the evaluation of environmental bioindicators (Dufrene and Legendre, 1997, Duelli and Obrist, 2003, Büchs et al., 2003). Despite that communities are often considered too much complex to permit general laws (Lawton, 1999), traditional community ecological research are now crucial in understanding and responding to many environmental problems including those posed by global change (Simberloff, 2004). Thus, assessing patterns of richness and diversity of animal communities through ecological gradients is becoming more and more recurrent in the field research of biogeography and landscape ecology (Rahbek, 1997). This has been particularly true for farmland birds (Pain and Pienkowski, 1997) but inventory of small mammal communities at different ecological scales have also increased in recent years (Canova and Fasola, 1991, Clark and Bunck, 1991, Kelt, 1996, Fitzgibbon, 1997, Millan de la Pena et al., 2003, Huitu et al., 2004).

These studies pointed out the fact that small mammals can be useful indicators of sustainability in terrestrial ecosystems, and thus have to be considered as a functional group of species assuming the role of seed dispersers, invertebrate consumers and preys for terrestrial and avian predators. Working on species assemblages needs to have efficient methods in estimating abundance of the different species but most animal groups are studied through indirect census methods. Trapping is the most common method used to study small mammals (Gurnell and Flowerdew, 1990). It has been successfully used to compare richness, composition and abundance of small mammal communities along ecological gradients (Kelt, 1996, Yu, 1994) and between different habitats (Canova and Fasola, 1991, Fitzgibbon, 1997, Tattersall et al., 2002, Huitu et al., 2004). However, the reliability of results depends on the efficiency of the trapping method used. Biases according to traps, bait used, species behaviour and sampling effort have often been reported (Blem et al, 1993, Yu, 1994, Yom-Tov and Wool, 1997, Sullivan et al., 2003). Sullivan et al. (2003) reported that removal-trapping can

disrupt small-mammal populations and yield spurious values for community characteristics. Moreover, simultaneous trapping on numerous sites is time-consuming and often unrealistic when we aim to assess the structure and the composition of small mammal community within a large diversity of landscape context (Millan de la Pena et al., 2003). This is why other indirect approaches, such as Barn Owl pellet analysis have been extensively used (Hanney, 1962, Glue, 1971, Perrin, 1982, Clark and Bunck, 1991, Millan de la Pena et al., 2003) owing to the generalist feeding behaviour of this raptor (Cooke et al, 1996). As for trapping techniques, biases associated to this second techniques have been reported (Glue, 1971).

In this paper we estimated richness, diversity and relative abundance of small mammal species in three agricultural landscape context by using trapping technique and on the basis of Barn Owl pellet analysis. Our aim was to compare composition and structure of the small mammal community derived from both techniques and to know which species may be used as bioindicators of agricultural changes according to the sampling method used.

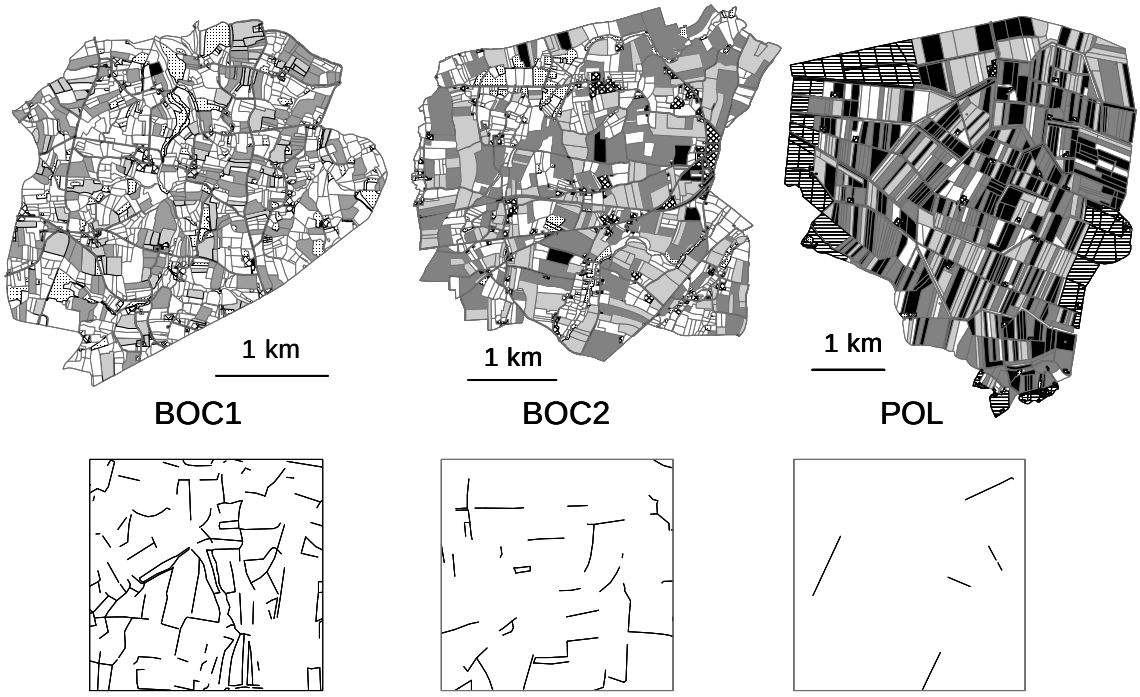
Study area and methods

Our study area was situated in northern Brittany, south of the Mont Saint Michel Bay (48° 36' N, 1° 32' W, western France). Three landscape units differing by their level of agricultural intensification and openness were chosen. Field surveys were carried out to determine land occupation in the 3 sites. Relative areas of land use cover and hedgerow network density were measured in the 3 landscape units using GIS (ArcView 8.2 software). Data are summarized in Figure AA.1. The first unit (BOC1) is slightly intensified with a very dense hedgerow network and large areas devoted to grassland. The second one (BOC2) is moderately intensified because of land reallotment. Crop fields are dominant over grasslands and the hedgerow network is fragmented. The third landscape unit is a high intensified polder (POL) with very few hedges and is oriented toward intensive cereals and vegetables production.

Hedges represent the main refuge habitat for small mammals in these kind of landscapes as fields are only colonised temporarily during the year. In each site, 8 trapping locations were chosen along the hedgerow network. Each of the 8 hedges per site were chosen to be representative of the hedgerow network and to present a certain heterogeneity in terms of physiognomy, layers, width or local environment. They were chosen to be as distant as possible from one another to avoid spatial autocorrelation in local abundance : the minimum distance between sampled hedges was 600m for BOC1 and 700m for BOC2 and POL.

Each of the 24 hedges were sampled 7 times from April 2003 to February 2004. We used a standardized trapping method (Spitz et al., 1974) consisting of a 100 m line of 34 baited live-traps placed every 3 m and checked at dawn twice in a period of 48 hours. We used INRA trap model efficient in catching both shrews and rodents.

At the level of sampled hedges, the total number of different individuals trapped with this method was used as an index of species abundance (Hansson, 1967). A mean relative abundance characteristic of each hedgerow network was computed by pooling total number of captures obtained from 7 trapping sessions on the 8 hedges of each landscape unit. Data were finally weighted by hedgerow density to be converted to relative abundance at the level of landscape units and expressed as total ind. x hedge length per hectare.



	BOC1	BOC2	POL
Hedgerow density (m/ha)	**98**	**48**	**12**
% Grasslands	**63,7**	**38,2**	**8,9**
% Crop fields	**36,3**	**63,8**	**91,1**
- Maize	*20,9*	*32,8*	*22,9*
- Vegetables	*0,2*	*0,6*	*35,6*
- Cereals	*15,2*	*30,4*	*32,6*

Figure AA.1
Soil occupation map, relative areas of land cover and density of the hedgerow network of the three landscape units (BOC1, BOC2 and POL).

Barn Owl pellet analysis was carried out on this same three landscape units. Pellets were collected in one or several resting places in each landscape unit and at different time along the year. Areas of the three units were respectively 1019 ha for BOC1, 1659 ha for BOC2 and 2544 ha for POL. As home range of the Barn Owl varies from 200 to 700 ha (Taylor, 1994), we can assume that Barn Owls collected their prey inside each landscape units. Pellets were finally gathered to obtain a reliable estimate of species composition and frequency in the diet of Barn Owls in the three units. The total number of pellets collected along the year was of 270 (BOC 1), 85 (BOC2) and 93 (POL) corresponding respectively to 1048, 342 and 415 preys identified on each of the three landscape units. Prey identification was made following the key provided by Chaline et al. (1974).

Species richness (S), Shannon-Weaver index of diversity (H) and equitability (=evenness) (J=H/lnS) were used to compare small mammals assemblages in the 3 sites (Shannon and Weaver, 1963 ; Magurran 1988 ; Silva, 2001). Shannon's diversity indexes were compared between sites using Hutcheson's test (Hutcheson 1970 ; Lande, 1996).

The different species belonging to the small mammal community were labelled as following : As : *Apodemus sylvaticus* (Wood mouse) (Linné 1758), Cg : *Clethrionomys glareolus* (Bank vole) (Schreber 1780), Mg : *Microtus agrestis* (Field vole) (Linné 1761), Ms : *Microtus subterraneus* (Common pine vole) (de Sélys-Longchamps 1836) and 4 Insectivorous species : Cr : *Crocidura russula* (White-toothed shrew) (Hermann 1780), Nf : *Neomys fodiens* (Aquatic shrew) (Pennant 1771), Sc : *Sorex coronatus* (Common shrew) (Millet 1828), Sm : *Sorex minutus* (Pigmy shrew) (Linné 1766).

Results

During the 11424 trap-nights effort, a total of 1379 captures was obtained from which 1191 (86%) were rodents and 188 (14%) were shrews. Details of captures are summarized in table 1. Concerning Barn Owl, 448 pellets were dissected and 1805 skulls of small mammals were identified as species and converted into species frequency (Table A.A.1).

We caught eight species in BOC 1 and BOC 2 and seven species in POL when using trapping techniques whereas we found ten species to be present in the 3 landscapes by using Barn Owl pellet analysis. A greater richness and a greater evenness of species frequencies was found by using pellet analysis leading to a higher diversity of the community estimated by this technique (Table A.A.1). From both techniques, a significant lower diversity was observed in POL than in the two other sites (BOC 1 and BOC 2). Two species (Ma and Mm) were only detected in Barn Owl pellets whereas the 8 others were found by both techniques (Table A.A.1).

Table A.A.1 : Small mammal species abundance and diversity in the three landscape units. Data are expressed as total captures of species (11424 trap-nights) and species frequency (percentage of total prey items) in Barn owl pellets. Richness (S), Shannon diversity index (H) and Evenness (J) are furnished for each landscape unit and each census technique.

		As	**Cg**	**Mg**	**Ms**	**Ma**	**Mm**	**Cr**	**Nf**	**Sc**	**Sm**	**S**	**S**	**H**	**J**
BOC I	Total captures	249	37	8	19	0	0	18	1	25	16	373	8	1.75	0.58
	Frequency in Barn Owl pellets	21.3	2.4	17.1	12.3	13.1	4.0	11.8	0.5	16.2	1.3	100	10	2.89	0.87
BOC II	Total captures	228	58	5	8	0	0	35	2	38	15	389	8	1.92	0.64
	Frequency in Barn Owl pellets	12.9	1.5	14.9	12.9	19.9	2.3	16.4	0.3	17.3	1.8	100	10	2.84	0.86
POL	Total captures	386	177	1	15	0	0	20	0	16	2	617	7	1.41**	0.50
	Frequency in Barn Owl pellets	8.4	0.3	6.0	28.2	9.0	2.2	26.8	0.2	16.7	2.2	100	10	2.60*	0.78

** Significance difference between diversity using Hutcheson's test ($p<0.01$).
Site III Significantly different from Sites I and II
* Significance difference between diversity using Hutcheson's test ($p<0.05$)
Site III significantly different from site I only

Two rodents species appeared largely dominant when relative frequencies were estimated from trapping data, whereas species frequencies calculated from pellet analysis were clearly better balanced (Fig. A.A.2).

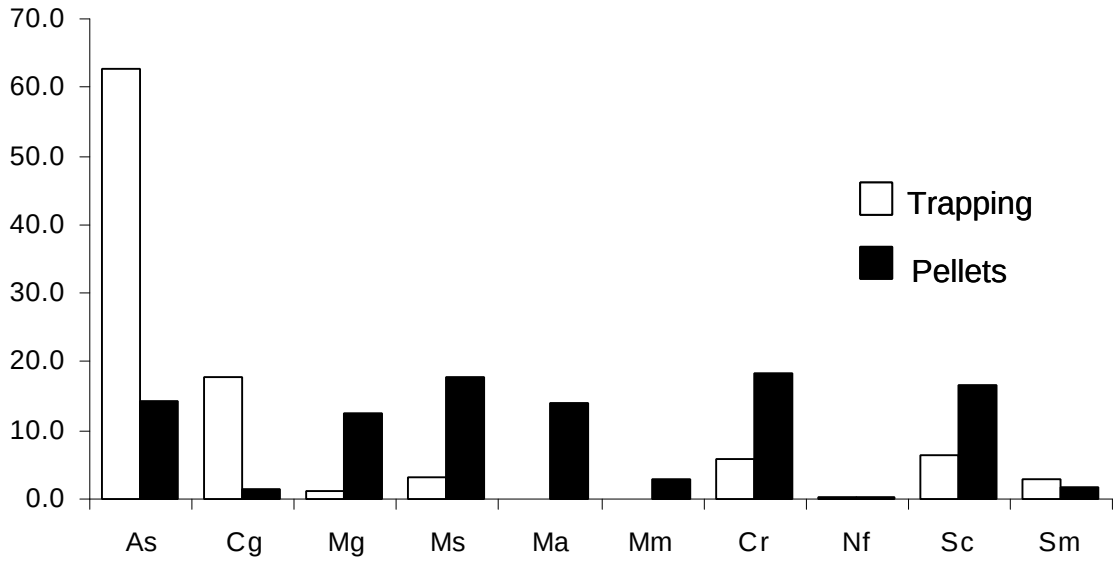


Figure A.A.2

Mean frequency (%) of the small mammal species performed from trapping and Barn Owl pellet analysis. Values were estimated by pooling data from the three landscape units.

Species availability estimated from trapping technique has been compared to species frequency in Barn Owl pellets along the gradient of the three landscape sites (Figure A.A.3). Availability of the different small species decreased markedly along this gradient according to the increasing fragmentation of the hedgerow network density from BOC 1 to POL ,. A similar significant decrease was observed for the frequency of four species (As, Cg, Mg, Nf) in Barn Owl pellets. One rodent (Ms) and three shrew species (Cr, Sc, Sm) were consumed in proportion that were not related to their availability calculated from trapping techniques. For example, Cr and Sm and Ms showed increasing frequency in pellets with landscape openness whereas their availability was decreasing according to the restriction of permanent habitats.

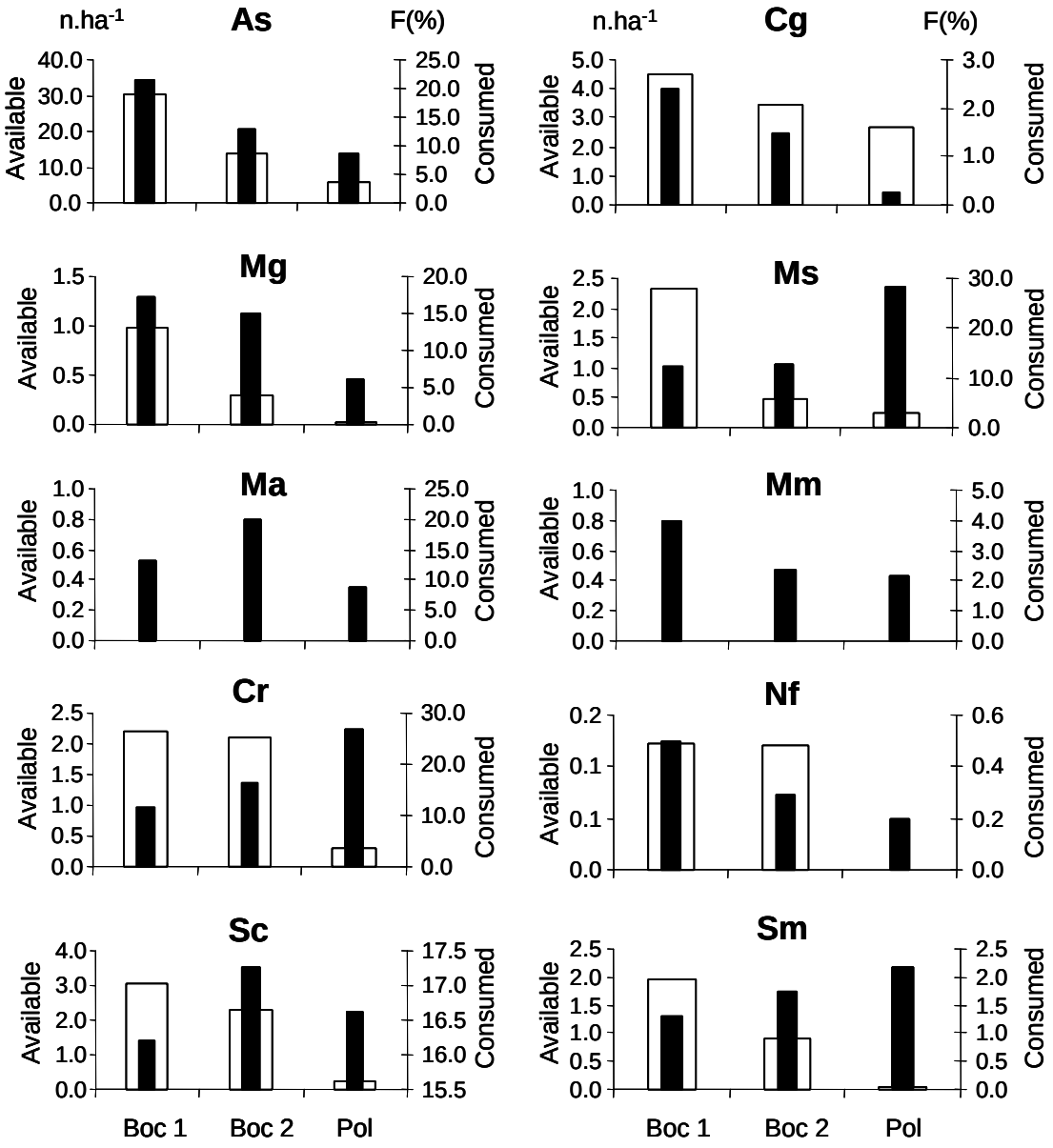


Figure A.A.3
Comparison of small mammal species availability (white bars) and their frequency in the diet of the Barn Owl (black bars) in the three landscape units. Species availability is expressed as total individuals caught on hedges x hedge length per hectare. Abundance in Barn Owl pellets is expressed as percentage of total prey items.

Discussion

Assessing small mammals abundance is most often performed through trapping, but biases associated to this technique are often discussed. A first bias is that some species would be trap-prone whereas others would be trap-shy (Blem et al., 1993; Yom-Tov and Wool, 1997). A second bias is that capture efficiency depends on the choice of selected places for trapping small mammals and many trapping plots would be needed to perceive this heterogeneity. In that respect, pellet analysis seemed a good answer as owls have strong fidelity to roosting places (Yom-Tov and Wool, 1997) but often change of hunting place and collect much larger prey samples than do traps. The Barn Owl is a generalist raptor , avoiding large forest areas and hunting in both open field and dense hedgerow network landscapes. It is known to focus almost exclusively on small mammals, and pellets are easily found and analyzed (Bunn et al., 1982, Taylor, 1994). For all these reasons, this is one of the most widely used method to study richness and composition of small mammal communities across ecological gradients (Giraudoux et al.1990, Clark and Bunck, 1991, Cooke et al., 1996).

We found more species detected and a greater diversity of the community when using pellets instead of trapping. The slower diversity obtained by trapping was mainly due to the dominance of two woodland rodents and the rarity of some species (some shrews and grassland rodents) occurring in traps. This agree totally with findings of Torre et al (2004) who reported that Owl pellets over sampled insectivores and grassland rodents and under sampled woodland rodents whereas live trapping over sampled woodland rodents and under sampled insectivores and grassland rodents. Barn Owls hunts on large open areas exploiting both fields and edges of woody habitats and more similar results would certainly be obtained with greater trapping effort including heterogeneity of grasslands, crop fields and field margin habitats. Such trapping effort is generally unrealistic and constitute the main limit of trapping technique for ecological studies performed on large scale ecological gradients.

Many authors have often discuss the biases associated to both techniques but few studies have reported data obtained with these techniques being performed simultaneously on the same area.

It is often claimed that Barn Owls show no food preferences (Bunn et al., 1982) and that the numbers of each species represented in the diet are a true reflection of prey abundance (Hanney, 1962 ; Glue, 1971). However, this claim is controversial. Glue (1971) believed that the species representation in Barn Owl pellets is proportional to the relative abundance of preys. Similarly, Mikkola (1983) concluded that the Barn Owl is a nonselective predator, whose diet reflects the abundance of small nocturnal mammal species within its hunting territory. However, in South Africa, Barn Owl preys determined from pellet analysis appeared to have a different proportion of species than samples of the same prey species obtained by trapping (Perrin, 1982), whereas the opposite was found in a similar comparison in Great Britain (Glue, 1967).

Yom-Tov and Wool (1997) validated pellet analysis as a suitable method for examining structure of small mammal assemblages at the landscape scale but recognized biases depending on the assumption that owls may not forage randomly according to habitat permeability and energy profitability of preys. There are still controversial opinions about this technique (Glue, 1971). The fact that studies based on predator sampling did not receive a general agreement is partly due to the absence of correlation with the real abundance of the preys. Up to now, probably only Yom-Tov and Wool (1997) tested through computer simulation. whether the distribution of prey species in pellets could reflect a random hunt. They concluded that Barn Owl do not hunt some species preferentially, but the contents of the pellets may be biased towards larger prey.

Recently, Love et al. (2000) studied the changes in the food of the British Barn Owl over 23 years period as an indicator of land management. In our study, despite important difference in species frequency associated to each technique, trapping and pellet analysis revealed interesting correlations between availability and consumption for some small mammal species in relation to land use changes.. An interesting result of our study is that most rodent species associated to the less disturbed and permanent habitats (hedges) could be good indicators of landscape changes as both techniques revealed very linked trajectories in their responses to land use intensification. A good relationship was also observed for the water shrew which may be explained by the fact that intensification of agriculture is often associated with degradation of wetlands habitats, but this has to be confirmed on larger ecological gradient regarding to the very low trapping records of this species. Bad relationships were observed for most of the shrew species (*Crocidura russula*, Sorex *coronatus* and *Sorex minutus*), two grassland rodents (*Microtus arvalis* and *Microtus*

subterraneus) and the harvest mouse (*Micromys minutus*) which is a rare species difficult to trap. Some of these species (i.e. *Crocidura russula*, *Microtus subterraneus* and *Microtus arvalis*) are known to use actively the crop field mosaic or to be typical of grassland areas (Millan de la Pena et al., 2003) which may probably explain why they are more easily detected by Barn Owl in open areas and under detected by trapping performed on field boundaries.

We can conclude from this study that pellet analysis seems to be more appropriated to evaluate the diversity of species being present at the landscape scale. Our study corroborates previous findings ascertaining that Barn Owls would tend to over sampled shrews and grassland species but, important trapping effort including a great variety of habitats should be conducted to validate more precisely the opposite biases associated with trapping techniques. Nevertheless, comparison of these two techniques indicate that some small mammal species seems to be eaten by Barn Owl proportionally to their availability and thus, may be used as useful indicators of spatio-temporal land use changes.

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Annexe 1 :

Liste et codes des OTEX (Orientation technico-économique).

	OTEX
Céréales et oléoprotéagineux	13
Cultures générales	14
Maraîchage	28
Fleurs et horticulture diverse	29
Viticulture d'appellation	37
Autre viticulture	38
Fruits et autres cultures permanentes	39
Bovins lait	41
Bovins viande	42
Bovins lait-viande	43
Ovins, caprins et autres herbivores	44
Granivores	50
Polyculture	60
Polyélevage à orientation herbivores	71
Polyélevage à orientation granivores	72
Grandes cultures et herbivores	81
Autres combinaisons cultures-élevage	82

Annexe 2 :

Relevés botaniques de la strate herbacée des 24 stations de piégeage.

An.2.1 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate herbacée des stations du site BOC1.

NOM ESPECE	BOC1-1	BOC1-2	BOC1-3	BOC1-4	BOC1-5	BOC1-6	BOC1-7	BOC1-8
Achillea millefolium millef.	0	0	0	0	0	1	0	0
Agrostis capillaris	0	0	0	0	0	0	0	0
Ajuga reptans	0	1	0	0	0	0	0	0
Anagallis arvensis	0	0	1	0	0	0	0	0
Anthoxantum odoratum	0	2	3	0	0	0	0	0
Angelica sylvestris	0	0	0	0	0	0	0	0
Arrhenatherum elatius	0	0	2	4	0	0	0	0
Arctium lappa	0	0	0	0	0	0	0	0
Arum maculatum	0	0	0	0	0	0	0	0
Arenaria serpyllifolia	0	0	0	0	0	0	0	0
Asparagus officinalis officina	0	0	0	0	0	0	0	0
Avena fatua	0	0	0	0	0	0	0	0
Bilderdykia convolvulus	0	0	1	0	0	0	0	0
Bryonia cretica ssp dioica	0	0	0	0	0	1	0	0
Bromus hordeaceus hordeaceus	0	0	0	0	0	0	0	0
Briza minor	0	0	2	0	0	0	0	0
Brachypodium sylvaticum sylvat	0	0	0	0	0	0	0	0
Bromus sterilis	1	0	3	0	0	2	0	2
Capsella bursa-pastoris	0	0	0	0	0	0	0	0
Cardamine flexuosa	0	0	3	0	0	0	0	0
Campanula rapunculus	0	0	0	0	0	0	0	0
Calystegia sepium sepium	0	0	2	0	0	0	0	0
Cerastium fontanum trivialis	0	0	0	0	0	0	0	0
Centaurea nigra nigra	0	0	0	0	0	0	0	0
Chaerophyllum temulentum	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0	1	2	0	0	0
Cirsium palustre	0	0	0	0	0	0	0	0
Cirsium vulgare	0	0	0	0	0	0	0	0
Clinopodium vulgare	0	2	0	0	0	0	0	0
Corylus avellana	0	0	0	0	0	0	0	0
Conopodium majus	0	3	0	1	0	0	2	1
Cruciata laevipes	0	0	0	0	0	0	0	0
Crataegus monogyna monogyna	0	3	0	0	0	0	2	0
Crepis vesicaria haenseleri	0	0	0	0	0	0	0	0
Cytisus scoparius scoparius	0	0	2	0	0	0	1	0
Daucus carota carota	0	0	0	0	0	0	0	0
Dactylis glomerata glomerata	3	3	0	4	2	4	4	3
Diplotaxis officinalis	0	0	0	0	0	0	0	0
Digitalis purpurea purpurea	0	2	3	1	0	1	1	0
Elymus atherica	0	0	0	0	0	0	0	0
Elymus repens repens	0	0	0	0	0	0	0	0
Epilobium tetragonum tetrag.	0	0	0	0	0	0	0	1
Equisetum arvense	0	0	0	0	0	0	0	0

Euphorbia amygdaloides amygd.	0	0	0	0	0	0	0	2
Eupathorium cannabium cannabiu	0	0	0	0	0	0	0	0
Euonymus europaeus	0	0	0	0	0	0	0	3
Festuca arundinacea ssp arund.	0	0	0	0	0	0	0	0
Festuca rubra rubra	0	0	0	0	0	0	0	0
Fraxinus excelsior excelsior	0	0	0	0	0	0	0	0
Fumaria muralis muralis	1	0	0	0	0	2	0	3
Fumaria officinalis officin.	0	0	4	2	0	0	0	0
Galium aparine	2	2	4	3	4	2	2	2
Galium mollugo	0	0	0	0	0	0	0	0
Galeopsis tetrahit	0	0	0	1	0	0	1	0
Geranium dissectum	0	0	0	0	0	0	0	0
Geranium molle	0	0	0	0	0	0	0	0
Geranium robertianum	0	0	0	0	0	0	0	1
Geum urbanum	0	1	0	0	0	0	0	0
Hedera helix helix	0	4	2	2	2	0	0	0
Heracleum sphondylium sphond.	0	0	0	0	0	0	0	0
Holcus lanatus	0	2	0	0	0	0	0	3
Holcus mollis mollis	3	4	0	2	0	3	4	2
Hypericum perforatum	0	0	0	0	0	0	0	0
Hypericum pulchrum	0	0	0	0	0	0	2	0
Hypochoeris radicata	0	0	0	0	0	0	1	0
Iris foetidissima	0	0	0	0	0	0	0	0
Lapsana communis communis	0	0	5	1	0	0	1	1
Leucanthemum vulgare	0	1	0	0	0	0	0	0
Ligustrum vulgare	0	0	0	0	0	0	0	0
Lolium perenne	0	0	0	0	0	0	0	0
Lonicera periclymenum pericly.	0	3	0	0	0	0	2	1
Mentha arvensis austriaca	0	0	0	0	0	0	0	0
Moehringia trinervia	0	0	0	0	0	0	0	0
Myosotis arvensis arvensis	0	0	0	0	0	0	0	0
Oenanthe crocata	0	0	0	0	0	0	0	0
Picris echioides	0	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	0	0
Potentilla anserina anserina	0	0	0	0	0	0	0	0
Poa pratensis	0	0	0	0	0	0	0	0
Potentilla sterilis	0	2	0	0	0	0	0	0
Poa trivialis trivialis	0	2	0	0	0	0	0	0
Prunus spinosa	0	1	0	0	0	0	0	0
Primula vulgaris vulgaris	0	0	0	0	0	0	0	0
Pteridium aquilinum	3	2	0	4	4	4	2	5
Pulicaria dysenterica	0	0	0	0	0	0	0	0
Quercus robur robur	0	4	2	0	1	0	1	0
Ranunculus acris acris	0	1	0	0	0	0	0	0
Ranunculus bulbosus	0	0	0	0	0	0	0	0
Ranunculus repens	0	0	0	0	0	0	0	0
Rosa arvensis	0	2	0	0	0	0	0	0
Rosa canina	0	1	0	0	0	0	0	0
Rosa species	0	2	0	0	0	0	0	0
Rumex acetosa	0	2	0	0	0	1	2	0
Rumex crispus	1	0	0	0	0	0	0	0

Rubus fruticosus	3	2	0	2	4	3	2	3
Rumex obtusifolius obtusif.	0	0	1	0	0	0	0	0
Sagina apetala apetala	4	0	0	0	0	0	0	0
Salix atrocinerea	0	0	0	0	0	0	0	0
Scrophularia nodosa	0	0	0	0	0	0	0	0
Senecio jacobea	0	0	0	0	0	0	0	0
Sedum telephium telephium	0	0	0	0	0	0	0	0
Senecio vulgaris	0	0	0	0	0	0	0	0
Silene dioica	0	0	0	0	0	0	0	0
Sisymbrium officinale	0	0	0	0	0	0	0	0
Sonchus arvensis arvensis	0	0	0	0	0	0	0	0
Sonchus asper asper	0	0	0	0	0	0	0	0
Solanum dulcamara	0	0	0	0	0	2	0	0
Solanum nigrum nigrum	0	0	1	0	0	0	0	0
Sonchus oleraceus	0	0	0	0	0	0	0	0
Solidago virgaurea	0	0	0	0	0	0	0	0
Stellaria holostea	1	2	0	0	0	1	2	0
Stellaria media media	0	0	0	0	0	1	0	0
Stachys officinalis	0	1	0	0	0	0	0	0
Stachys sylvatica	0	0	0	0	0	0	0	0
Symphitum officinale officin.	0	0	0	0	0	0	0	0
Tamus communis	0	1	0	0	2	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0
Teucrium scorodonia scorod.	2	3	0	0	0	2	4	0
Trifolium hybridum	0	0	0	0	0	0	0	0
Urtica dioica	0	2	0	0	4	0	0	0
Veronica arvensis	0	0	0	0	0	0	0	0
Veronica chamaedrys chamaed.	0	2	0	0	0	0	0	0
Vicia hirsuta	0	0	0	0	0	0	0	0
Viola riviniana	0	3	0	0	0	0	3	0
Vicia sativa ssp nigra	0	0	0	0	0	0	0	0
Vicia sativa ssp sativa	0	0	0	0	0	0	0	0
Vicia tetrasperma	0	0	0	0	0	0	0	0

An.2.2 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate herbacée des stations du site BOC2.

NOMESPECE	BOC2-1	BOC2-2	BOC2-3	BOC2-4	BOC2-5	BOC2-6	BOC2-7	BOC2-8
Achillea millefolium millef.	1	0	0	0	0	0	0	0
Agrostis capillaris	0	0	0	0	1	0	0	0
Ajuga reptans	0	0	0	0	0	0	0	0
Anagallis arvensis	0	0	0	0	0	0	0	0
Anthoxantum odoratum	2	0	0	0	1	0	0	2
Angelica sylvestris	0	0	0	0	1	0	0	1
Arrhenatherum elatius	5	3	1	2	2	4	5	0
Arctium lappa	0	0	0	0	0	0	0	0
Arum maculatum	0	0	0	0	0	0	0	0
Arenaria serpyllifolia	0	0	0	0	0	0	0	0
Asparagus officinalis officina	0	0	0	0	0	0	0	0
Avena fatua	0	0	0	0	1	0	0	0
Bilderdykia convolvulus	0	0	0	0	0	0	0	0
Bryonia cretica ssp dioica	0	0	0	0	0	1	0	0
Bromus hordeaceus hordeaceus	2	0	0	0	1	0	0	0
Briza minor	0	0	0	0	0	0	0	0
Brachypodium sylvaticum sylvat	0	0	0	0	0	0	0	0
Bromus sterilis	1	2	0	2	0	0	2	0
Capsella bursa-pastoris	0	0	0	0	0	0	0	0
Cardamine flexuosa	0	0	1	0	0	0	0	0
Campanula rapunculus	0	0	0	0	0	0	1	0
Calystegia sepium sepium	0	2	1	0	0	2	0	0
Cerastium fontanum trivialis	0	0	0	0	1	0	0	0
Centaurea nigra nigra	0	0	0	0	2	0	0	0
Chaerophyllum temulentum	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	0	0	0	1
Cirsium palustre	0	0	0	0	2	0	0	1
Cirsium vulgare	0	0	0	2	0	0	0	1
Clinopodium vulgare	0	0	0	0	0	0	0	0
Corylus avellana	0	1	0	0	0	0	0	0
Conopodium majus	1	0	0	0	0	1	0	0
Cruciata laevipes	0	0	0	0	2	2	2	3
Crataegus monogyna monogyna	0	0	0	0	2	0	0	0
Crepis vesicaria haenseleri	0	0	0	0	0	0	0	0
Cytisus scoparius scoparius	0	0	0	0	0	0	0	0
Daucus carota carota	0	0	0	0	0	0	0	1
Dactylis glomerata glomerata	4	1	2	4	5	3	3	4
Diplotaxis officinalis	0	0	0	0	0	0	0	0
Digitalis purpurea purpurea	0	0	0	0	2	0	0	0
Elymus atherica	0	0	0	0	0	0	0	0
Elymus repens repens	1	2	0	3	0	0	0	0
Epilobium tetragonum tetrag.	0	0	0	0	2	1	0	0
Equisetum arvense	0	0	0	0	3	0	0	0
Euphorbia amygdaloides amygd.	0	0	0	0	0	0	0	0
Eupathorium cannabium cannabiu	0	0	0	0	0	0	0	0
Euonymus europaeus	1	0	0	1	0	0	0	0
Festuca arundinacea ssp arund.	0	0	0	0	0	0	0	0

Festuca rubra rubra	0	0	0	0	0	0	0	0
Fraxinus excelsior excelsior	0	0	0	0	0	0	0	0
Fumaria muralis muralis	0	1	0	0	0	0	0	0
Fumaria officinalis officin.	0	0	0	0	0	0	0	0
Galium aparine	2	4	1	2	1	0	3	3
Galium mollugo	1	0	0	0	0	0	0	2
Galeopsis tetrahit	0	0	0	0	0	0	0	0
Geranium dissectum	1	0	0	0	1	0	0	0
Geranium molle	0	0	0	0	0	0	0	0
Geranium robertianum	0	0	0	0	3	0	2	0
Geum urbanum	0	0	0	0	0	0	3	0
Hedera helix helix	0	2	5	2	3	0	1	2
Heracleum sphondylium sphond.	1	0	1	1	2	1	1	0
Holcus lanatus	2	0	0	0	3	2	0	3
Holcus mollis mollis	1	0	1	3	3	2	0	0
Hypericum perforatum	1	0	0	0	0	0	0	0
Hypericum pulchrum	0	0	0	0	0	0	0	0
Hypochoeris radicata	0	0	0	0	1	0	0	0
Iris foetidissima	0	0	0	0	0	0	0	0
Lapsana communis communis	1	1	0	0	1	1	1	1
Leucanthemum vulgare	0	0	0	0	0	0	0	0
Ligustrum vulgare	0	0	0	0	0	0	0	0
Lolium perenne	0	0	0	0	0	0	0	0
Lonicera periclymenum pericly.	0	0	0	1	2	0	0	2
Mentha arvensis austriaca	0	0	0	0	0	0	0	0
Moehringia trinervia	0	0	0	0	3	0	0	0
Myosotis arvensis arvensis	0	0	0	0	0	0	0	0
Oenanthe crocata	0	0	0	0	1	0	0	0
Picris echioides	0	0	0	0	0	0	0	0
Plantago lanceolata	0	0	0	0	0	0	0	0
Potentilla anserina anserina	0	0	0	0	2	0	0	0
Poa pratensis	0	0	0	0	0	0	0	0
Potentilla sterilis	0	0	0	0	0	0	0	0
Poa trivialis trivialis	0	0	0	1	1	0	0	0
Prunus spinosa	0	0	0	0	1	0	0	0
Primula vulgaris vulgaris	0	0	0	0	2	0	0	0
Pteridium aquilinum	0	1	0	2	3	5	2	0
Pulicaria dysenterica	0	0	0	0	1	0	0	0
Quercus robur robur	2	0	1	1	0	0	0	2
Ranunculus acris acris	0	0	0	0	0	0	0	0
Ranunculus bulbosus	0	0	0	0	0	0	0	0
Ranunculus repens	0	0	1	0	1	0	2	2
Rosa arvensis	0	0	0	0	0	0	0	0
Rosa canina	0	0	0	0	0	0	0	0
Rosa species	0	0	0	0	0	0	0	0
Rumex acetosa	1	0	0	1	2	0	1	0
Rumex crispus	1	0	0	0	0	0	0	1
Rubus fruticosus	0	0	3	0	3	0	0	0
Rumex obtusifolius obtusif.	0	0	0	0	0	0	0	0
Sagina apetala apetala	0	0	0	0	0	0	0	0
Salix atrocinerea	0	0	1	0	0	0	0	0

Scrophularia nodosa	0	0	0	0	2	0	0	0
Senecio jacobea	0	0	0	0	0	0	0	0
Sedum telephium telephium	0	0	0	0	0	0	1	0
Senecio vulgaris	0	1	0	0	0	0	0	0
Silene dioica	0	0	0	0	0	0	0	0
Sisymbrium officinale	0	0	0	0	0	0	0	0
Sonchus arvensis arvensis	0	0	0	0	0	0	0	0
Sonchus asper asper	0	2	0	0	1	0	0	0
Solanum dulcamara	0	0	0	0	0	0	0	0
Solanum nigrum nigrum	0	0	0	0	0	0	0	0
Sonchus oleraceus	0	0	0	0	0	0	0	0
Solidago virgaurea	0	0	0	0	0	0	0	1
Stellaria holostea	2	2	0	0	3	1	2	3
Stellaria media media	0	0	0	0	0	0	0	0
Stachys officinalis	0	0	0	0	0	0	0	0
Stachys sylvatica	0	0	0	0	1	0	1	0
Symphitum officinale officin.	1	0	0	0	0	0	0	0
Tamus communis	0	0	1	0	3	0	0	0
Taraxacum officinale	0	0	0	0	0	0	1	0
Teucrium scorodonia scorod.	0	0	0	0	3	1	1	2
Trifolium hybridum	0	0	0	0	3	0	0	0
Urtica dioica	2	4	3	4	2	2	3	2
Veronica arvensis	0	0	0	0	0	0	0	0
Veronica chamaedrys chamaed.	0	0	0	0	2	0	1	1
Vicia hirsuta	0	0	0	0	2	0	0	0
Viola riviniana	0	0	0	0	0	0	0	0
Vicia sativa ssp nigra	2	0	0	0	0	1	0	2
Vicia sativa ssp sativa	0	0	0	0	1	0	0	0
Vicia tetrasperma	0	0	0	0	2	0	0	1

An.2.3 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate herbacée des stations du site POL.

NOMESPECE	POL-1	POL-2	POL-3	POL-4	POL-5	POL-6	POL-7	POL-8
Achillea millefolium millef.	0	0	0	0	0	0	2	1
Agrostis capillaris	0	0	0	0	0	0	0	0
Ajuga reptans	0	0	0	0	0	0	0	0
Anagallis arvensis	0	0	0	0	0	0	0	0
Anthoxantum odoratum	0	0	0	0	0	0	0	0
Angelica sylvestris	0	0	0	0	0	0	0	0
Arrhenatherum elatius	0	0	0	0	0	0	0	3
Arctium lappa	0	1	0	0	0	0	0	0
Arum maculatum	0	2	0	0	0	0	0	0
Arenaria serpyllifolia	0	0	0	0	0	0	2	0
Asparagus officinalis officina	0	0	0	0	0	1	2	0
Avena fatua	0	0	0	0	0	0	0	0
Bilderdykia convolvulus	0	0	0	0	0	0	0	0
Bryonia cretica ssp dioica	0	1	2	0	0	0	0	1
Bromus hordeaceus hordeaceus	0	0	0	0	0	0	3	0
Briza minor	0	0	0	0	0	0	0	0
Brachypodium sylvaticum sylvat	1	0	0	0	0	0	0	0
Bromus sterilis	0	3	3	4	4	4	0	3
Capsella bursa-pastoris	0	0	0	0	0	1	0	0
Cardamine flexuosa	0	0	0	0	0	0	0	0
Campanula rapunculus	0	0	0	0	0	0	0	0
Calystegia sepium sepium	0	2	0	0	0	0	0	0
Cerastium fontanum trivialis	0	0	0	2	0	0	1	0
Centaurea nigra nigra	0	0	0	0	0	0	0	0
Chaerophyllum temulentum	0	0	0	0	0	0	0	1
Cirsium arvense	2	2	0	0	1	0	0	0
Cirsium palustre	0	0	0	0	0	0	0	0
Cirsium vulgare	0	0	1	0	0	0	0	0
Clinopodium vulgare	0	0	0	0	0	0	0	0
Corylus avellana	0	0	0	0	0	0	0	0
Conopodium majus	0	0	0	0	0	0	0	0
Cruciata laevipes	0	0	0	0	0	0	0	0
Crataegus monogyna monogyna	0	0	0	0	0	0	0	2
Crepis vesicaria haenseleri	0	0	0	1	0	0	1	0
Cytisus scoparius scoparius	0	0	0	0	0	0	0	0
Daucus carota carota	0	0	0	2	1	2	2	0
Dactylis glomerata glomerata	1	3	0	0	0	2	0	0
Diplotaxis officinalis	0	0	0	0	0	0	2	0
Digitalis purpurea purpurea	0	0	0	0	0	0	0	0
Elymus atherica	0	0	0	4	0	3	2	0
Elymus repens repens	5	5	3	0	4	0	0	0
Epilobium tetragonum tetrag.	0	0	0	0	0	0	0	0
Equisetum arvense	0	0	0	0	0	0	0	0
Euphorbia amygdaloides amygd.	0	0	0	0	0	0	0	0
Eupathorium cannabium cannabiu	0	2	0	0	0	0	0	1
Euonymus europaeus	0	0	0	0	0	0	0	0
Festuca arundinacea ssp arund.	0	0	0	5	0	0	0	1

Festuca rubra rubra	0	0	0	0	0	0	5	1
Fraxinus excelsior excelsior	0	0	0	0	0	0	0	3
Fumaria muralis muralis	0	0	0	0	0	0	0	0
Fumaria officinalis officin.	0	0	0	0	0	0	0	0
Galium aparine	4	4	5	2	3	0	0	3
Galium mollugo	0	0	0	0	0	2	0	0
Galeopsis tetrahit	0	0	0	0	0	0	0	0
Geranium dissectum	0	0	0	0	0	0	0	0
Geranium molle	0	0	0	0	0	1	0	0
Geranium robertianum	0	0	0	0	0	0	0	3
Geum urbanum	0	0	0	0	0	0	0	0
Hedera helix helix	3	4	0	4	5	0	0	5
Heracleum sphondylium sphond.	0	0	0	0	0	4	0	2
Holcus lanatus	0	0	0	0	0	0	0	0
Holcus mollis mollis	0	0	0	0	0	0	0	2
Hypericum perforatum	0	0	0	0	0	0	0	1
Hypericum pulchrum	0	0	0	0	0	0	0	0
Hypochoeris radicata	0	0	0	0	0	0	0	0
Iris foetidissima	0	0	0	1	0	0	0	0
Lapsana communis communis	0	0	0	0	2	0	0	0
Leucanthemum vulgare	0	0	0	0	0	0	2	0
Ligustrum vulgare	0	0	0	0	0	0	0	3
Lolium perenne	0	0	0	0	0	5	4	0
Lonicera periclymenum pericly.	0	0	0	0	0	0	0	0
Mentha arvensis austriaca	0	0	0	2	0	0	0	0
Moehringia trinervia	0	0	0	0	0	0	0	0
Myosotis arvensis arvensis	0	0	0	0	1	0	0	0
Oenanthe crocata	0	0	0	0	0	0	0	0
Picris echioides	2	0	0	3	0	0	0	0
Plantago lanceolata	0	0	0	1	0	0	2	0
Potentilla anserina anserina	0	0	0	0	0	0	0	0
Poa pratensis	0	0	0	2	2	3	0	0
Potentilla sterilis	0	0	0	0	0	0	0	0
Poa trivialis trivialis	0	0	0	0	0	0	0	0
Prunus spinosa	0	0	1	0	0	0	0	0
Primula vulgaris vulgaris	0	0	0	0	0	0	0	0
Pteridium aquilinum	0	0	0	0	0	0	0	0
Pulicaria dysenterica	0	0	0	0	0	0	0	0
Quercus robur robur	0	0	0	0	0	0	0	1
Ranunculus acris acris	0	0	0	0	0	0	0	0
Ranunculus bulbosus	0	0	0	0	0	0	1	0
Ranunculus repens	0	0	0	0	0	3	0	0
Rosa arvensis	0	0	0	0	0	0	0	0
Rosa canina	0	0	0	0	0	0	0	0
Rosa species	0	0	0	0	0	0	0	0
Rumex acetosa	0	0	0	0	0	0	0	0
Rumex crispus	0	0	0	0	0	0	0	0
Rubus fruticosus	4	4	4	0	0	0	0	4
Rumex obtusifolius obtusif.	0	0	0	0	0	0	0	0
Sagina apetala apetala	0	0	0	0	0	0	0	0
Salix atrocinerea	0	0	0	0	0	0	0	0

Scrophularia nodosa	0	0	0	0	0	0	0	0
Senecio jacobea	0	0	0	0	0	1	0	0
Sedum telephium telephium	0	0	0	0	0	0	0	0
Senecio vulgaris	0	0	0	0	0	0	0	0
Silene dioica	0	0	0	0	0	0	1	0
Sisymbrium officinale	0	0	0	0	0	1	0	0
Sonchus arvensis arvensis	0	0	0	0	1	0	0	0
Sonchus asper asper	0	0	0	0	0	0	0	1
Solanum dulcamara	0	0	0	0	0	0	0	0
Solanum nigrum nigrum	0	0	0	0	0	0	0	0
Sonchus oleraceus	0	0	1	2	0	0	0	0
Solidago virgaurea	0	0	0	0	0	0	0	0
Stellaria holostea	0	0	0	0	0	0	0	0
Stellaria media media	0	0	0	0	0	0	0	0
Stachys officinalis	0	0	0	0	0	0	0	0
Stachys sylvatica	0	0	0	0	0	0	0	2
Symphitum officinale officin.	0	0	2	0	0	0	0	1
Tamus communis	0	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	1	1	0	2	0
Teucrium scorodonia scorod.	0	0	0	0	0	0	0	0
Trifolium hybridum	0	0	0	0	0	0	0	0
Urtica dioica	3	4	4	0	2	4	0	3
Veronica arvensis	0	0	0	1	0	1	0	0
Veronica chamaedrys chamaed.	0	0	0	0	0	0	0	0
Vicia hirsuta	0	0	0	0	0	0	0	0
Viola riviniana	0	0	0	0	0	0	0	3
Vicia sativa ssp nigra	0	0	0	0	0	0	0	0
Vicia sativa ssp sativa	0	0	0	2	0	0	0	0
Vicia tetrasperma	0	0	0	0	0	0	0	0

Annexe 3 : Relevés botaniques de la strate arbustive des 24 stations de piégeage.

An.3.1 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate arbustive des stations du site BOC1.

NOM ESPECE	BOC1-1	BOC1-2	BOC1-3	BOC1-4	BOC1-5	BOC1-6	BOC1-7	BOC1-8
Castanea sativa	5	0	0	0	0	0	4	2
Corylus avellana	0	2	2	2	2	5	0	0
Crataegus monogyna monogyna	0	0	0	1	1	0	0	0
Cytisus scoparius scoparius	0	0	0	3	0	0	0	0
Euonymus europaeus	0	0	0	1	2	0	1	0
Fraxinus excelsior excelsior	0	0	2	0	0	0	0	0
Ligustrum vulgare	0	0	0	0	0	0	0	0
Mespilus germanica	0	0	0	1	0	0	0	0
Populus x canadensis	0	0	0	0	0	0	0	0
Prunus avium	0	0	0	0	0	0	1	0
Prunus spinosa	0	0	0	0	0	0	0	0
Pyrus communis	0	0	0	1	0	0	0	0
Quercus robur robur	0	0	0	0	0	0	1	2
Rosa arvensis	0	0	0	2	0	0	0	0
Rosa canina	0	0	0	0	0	0	0	0
Rubus fruticosus	0	0	0	0	0	0	0	0
Salix atrocinerea	0	0	0	0	0	0	0	0
Sambucus nigra	0	0	0	1	0	0	0	0
Ulex europaeus europaeus	0	0	0	0	0	0	0	0
Ulmus minor	0	0	0	0	0	0	0	0

An.3.2 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate arbustive des stations du site BOC2.

NOM ESPECE	BOC2-1	BOC2-2	BOC2-3	BOC2-4	BOC2-5	BOC2-6	BOC2-7	BOC2-8
Castanea sativa	0	2	0	4	3	3	1	0
Corylus avellana	0	1	4	2	3	0	0	0
Crataegus monogyna monogyna	0	0	2	0	3	1	0	0
Cytisus scoparius scoparius	0	0	0	0	2	0	0	0
Euonymus europaeus	0	0	0	1	0	0	0	0
Fraxinus excelsior excelsior	0	0	0	0	0	0	0	0
Ligustrum vulgare	0	0	0	0	0	0	0	0
Mespilus germanica	0	0	0	0	0	0	0	0
Populus x canadensis	0	0	0	0	0	0	0	0
Prunus avium	0	0	0	1	0	0	0	0
Prunus spinosa	0	0	1	0	0	0	0	0
Pyrus communis	0	0	0	0	1	0	0	0
Quercus robur robur	0	0	2	3	3	0	3	4
Rosa arvensis	0	0	0	0	0	0	0	0
Rosa canina	0	0	0	1	1	1	0	0
Rubus fruticosus	0	0	3	0	3	4	4	0
Salix atrocinerea	0	0	0	0	0	0	0	2
Sambucus nigra	0	0	0	1	0	0	0	0
Ulex europaeus europaeus	0	0	0	0	1	0	0	0
Ulmus minor	0	0	0	0	3	0	0	0

An.3.3 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate arbustive des stations du site POL.

NOM ESPECE	POL-1	POL-2	POL-3	POL-4	POL-5	POL-6	POL-7	POL-8
Castanea sativa	0	0	0	0	0	0	0	0
Corylus avellana	0	0	0	0	0	0	0	0
Crataegus monogyna monogyna	2	0	1	0	0	5	1	0
Cytisus scoparius scoparius	0	0	0	0	0	0	0	0
Euonymus europaeus	0	0	0	0	0	0	0	0
Fraxinus excelsior excelsior	0	0	0	0	0	0	0	0
Ligustrum vulgare	0	0	0	0	0	0	0	1
Mespilus germanica	0	0	0	0	0	0	0	0
Populus x canadensis	0	0	0	3	0	0	0	0
Prunus avium	0	0	0	0	0	0	0	0
Prunus spinosa	0	0	0	0	0	0	0	0
Pyrus communis	0	0	0	0	0	0	0	0
Quercus robur robur	0	0	0	0	0	0	0	0
Rosa arvensis	0	0	0	0	0	0	0	0
Rosa canina	0	0	0	0	0	0	0	0
Rubus fruticosus	0	4	3	0	0	0	3	0
Salix atrocinerea	0	0	0	0	0	0	0	0
Sambucus nigra	0	0	1	0	0	1	0	0
Ulex europaeus europaeus	0	0	0	0	0	0	0	0
Ulmus minor	5	5	0	5	5	0	5	0

Annexe 4 :

Relevés botaniques de la strate arborescente des 24 stations de piégeage.

An.4.1 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate arborescente des stations du site BOC1.

NOM ESPECE	BOC1-1	BOC1-2	BOC1-3	BOC1-4	BOC1-5	BOC1-6	BOC1-7	BOC1-8
Castanea sativa	0	3	3	3	1	2	0	4
Crataegus monogyna monogyna	0	0	0	0	0	0	0	0
Fraxinus excelsior excelsior	0	0	0	0	0	0	0	0
Populus x canadensis	0	0	0	0	0	0	0	0
Prunus avium	0	0	0	0	0	1	1	0
Quercus robur robur	0	3	3	3	4	1	1	0
Salix atrocinerea	0	0	0	0	0	0	0	0
Ulmus minor	0	0	0	0	0	0	0	0

An.4.2 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate arborescente des stations du site BOC2.

NOM ESPECE	BOC2-1	BOC2-2	BOC2-3	BOC2-4	BOC2-5	BOC2-6	BOC2-7	BOC2-8
Castanea sativa	2	2	0	4	3	3	0	0
Crataegus monogyna monogyna	0	0	3	0	0	0	0	0
Fraxinus excelsior excelsior	0	0	0	0	0	0	0	0
Populus x canadensis	0	0	0	0	1	0	0	0
Prunus avium	0	0	0	0	0	0	0	0
Quercus robur robur	0	0	0	3	3	2	3	4
Salix atrocinerea	0	0	2	0	0	0	0	0
Ulmus minor	0	0	0	0	0	0	0	0

An.4.3 Liste des espèces végétales issue des relevés botaniques effectuées dans la strate arborescente des stations du site POL.

NOM ESPECE	POL-1	POL-2	POL-3	POL-4	POL-5	POL-6	POL-7	POL-8
Castanea sativa	0	0	0	0	0	0	0	0
Crataegus monogyna monogyna	0	0	0	0	0	0	0	2
Fraxinus excelsior excelsior	0	0	2	0	2	0	0	5
Populus x canadensis	0	2	4	3	0	1	0	2
Prunus avium	0	0	0	0	0	0	0	0
Quercus robur robur	0	0	0	0	0	0	0	0
Salix atrocinerea	0	0	0	0	0	0	0	0
Ulmus minor	0	5	0	5	5	0	0	0

Annexe 5 :

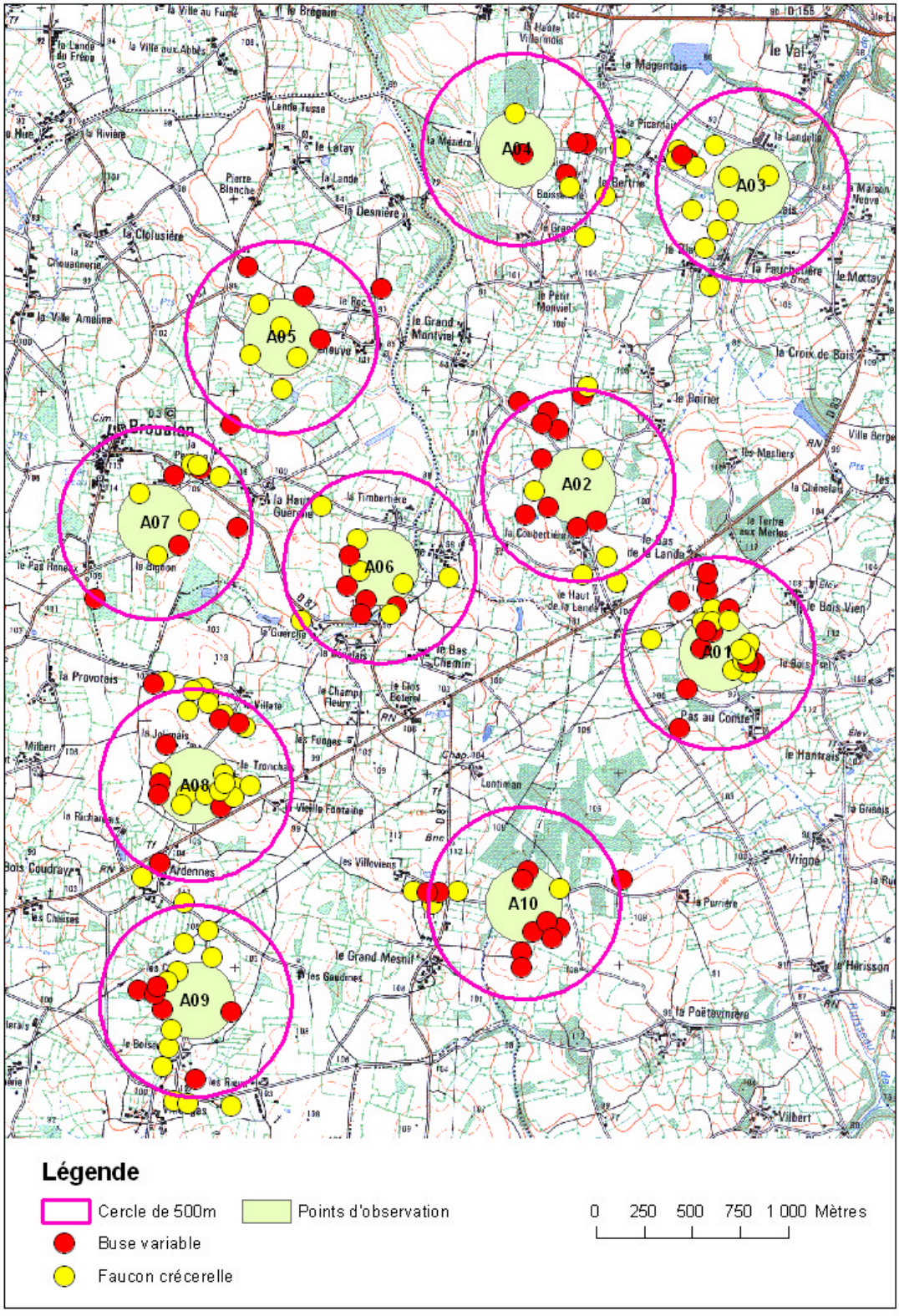
Mesures d'hétérogénéité (logiciel Chloé) dans un rayon de 200, 300, 400 ou 500 m autour de chacune des 24 stations de piégeage.

	Hétérogénéité			
Station	200m	300m	400m	500m
BOC1-1	1,197	1,534	1,595	1,688
BOC1-2	1,362	1,418	1,461	1,426
BOC1-3	1,169	1,450	1,504	1,363
BOC1-4	0,916	1,248	1,452	1,595
BOC1-5	0,687	1,054	1,343	1,534
BOC1-6	1,375	1,676	1,891	1,975
BOC1-7	1,374	1,300	1,343	1,433
BOC1-8	1,345	1,540	1,522	1,531
BOC2-1	0,895	1,258	1,505	1,617
BOC2-2	0,993	1,107	1,230	1,338
BOC2-3	1,099	1,364	1,511	1,533
BOC2-4	0,318	0,554	0,830	1,035
BOC2-5	1,940	2,218	2,148	2,045
BOC2-6	1,749	1,822	2,023	1,905
BOC2-7	0,289	0,887	1,040	1,318
BOC2-8	1,156	1,778	1,771	1,880
POL-1	1,569	1,707	1,720	1,816
POL-2	1,494	1,555	1,471	1,485
POL-3	1,139	1,353	1,527	1,590
POL-4	1,386	1,443	1,555	1,598
POL-5	1,208	1,416	1,503	1,563
POL-6	1,442	1,505	1,557	1,677
POL-7	1,644	1,619	1,615	1,505
POL-8	1,499	1,685	1,669	1,637

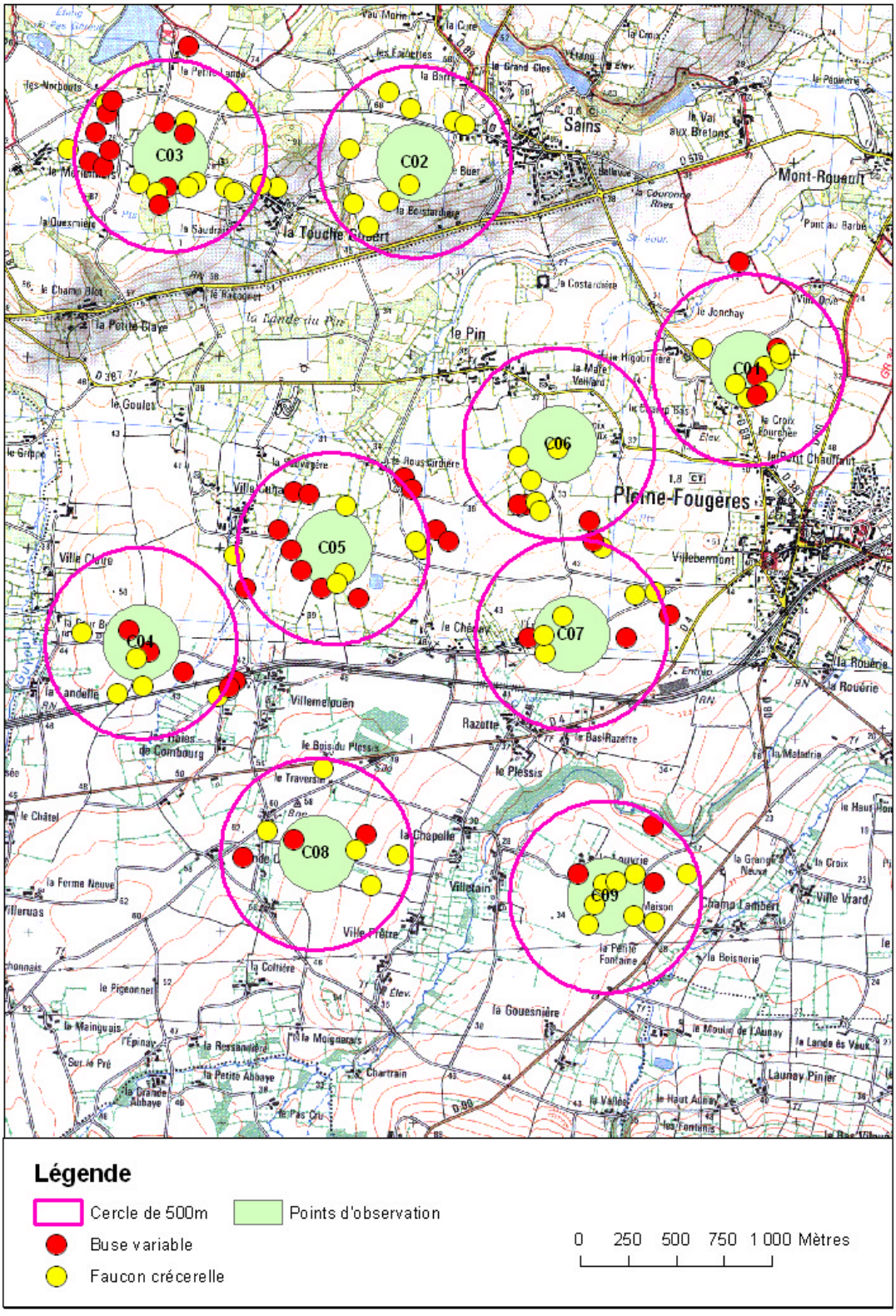
Annexe 6 :

Cumul et positionnement géographique (SIG) des rapaces observés à l'intérieur des cercles de 500m de rayon autour des points d'observation (Novembre 2004-Octobre 2005).

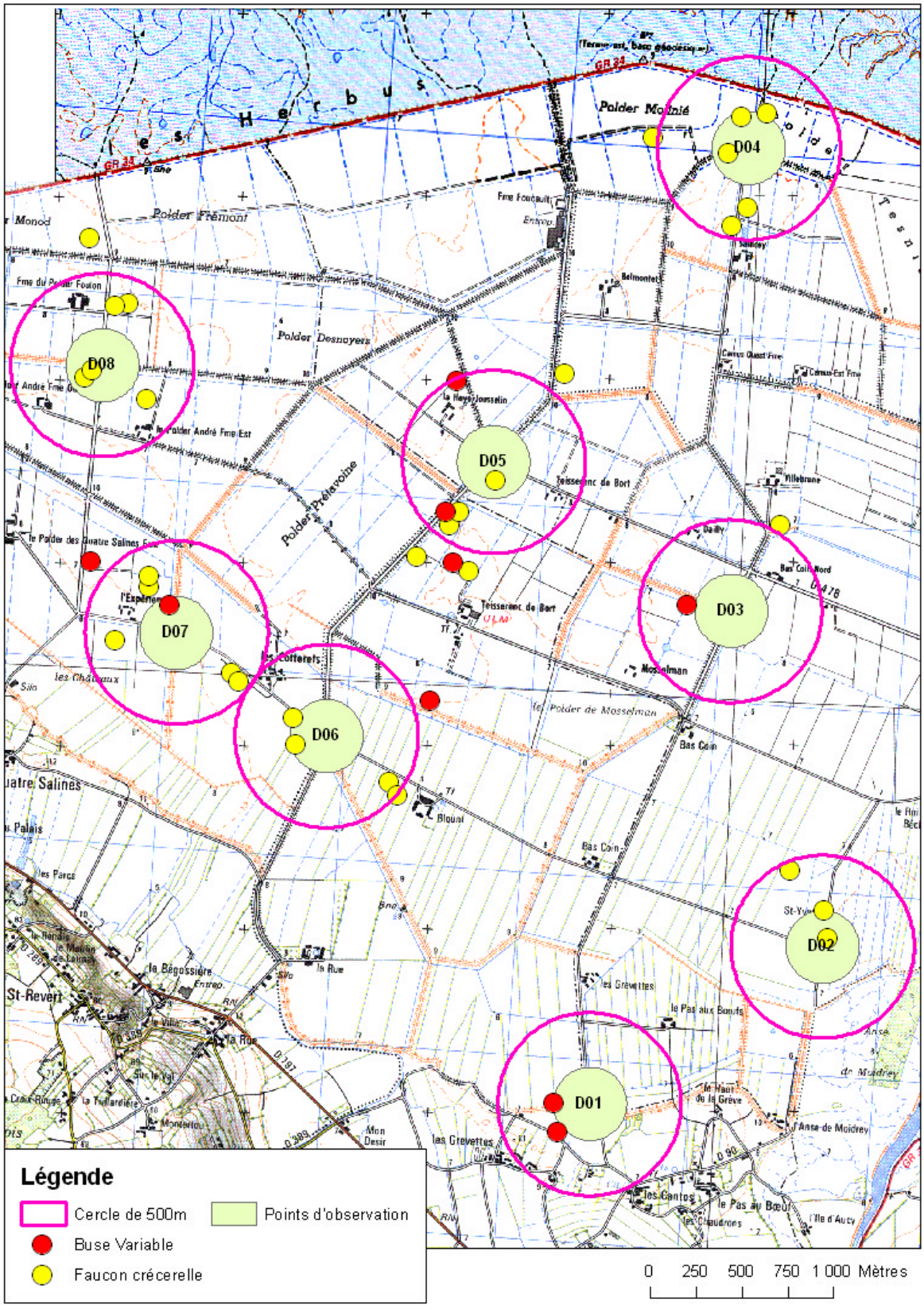
An.6.1. SITE BOC1 (Points d'observations notés A01 à A10)



An.6.2. SITE BOC2 (Points d'observations notés C01 à C09)



An.6.3. SITE POL (Points d'observations notés D01 à D08)



ACTIVITES PENDANT LA THESE :

Enseignement :

350 heures de TP et TD à l'université de Rennes 1, en niveau DEUG et Maîtrise

- Biologie Animale
  - Plathelminthes
  - Mollusques
  - Annélides
  - Crustacés
  - Tégument des Vertébrés
  - Embryologie des Amphibiens
  - Embryologie des Oiseaux
- Ecologie
  - La forêt
  - Invertébrés de la litière
  - Indices biotiques
  - Invertébrés aquatiques
  - Ecologie du paysage
- Encadrement de Travaux d'étude et de recherche

Formations :

- Anglais
- Anglais (stage intensif)
- Systèmes d'Informations Géographiques
- Modèle linéaire
- Séminaire Hétérogénéité
- Stages du Centre d'Initiation à l'Enseignement Supérieur
- Doctoriales Bretagne

- Stage analyse de données dans le labo de Pierre Legendre (Montréal)

Recherche :

- Article de DEA publié dans *Developmental Psychobiology*
  Nongenomic inheritance of emotional reactivity in Japanese quail.
  Marie-Annick Richard-Yris, Nadia Michel, Aline Bertin
  Developmental Psychobiology (2005)
  Volume 46, Issue 1, Pages 1-12
- Articles de thèse (1 accepté dans *Acta Oecologica*, 3 soumis)
- Articles en préparation (Chapitre 4 + Article sur notions Spécialiste-Généraliste)
- Colloques
  - Journée d'Ecologie Fonctionnelle, Rennes, Mars 2004
  - Annual Meeting of the British Ecological Society, Lancaster (UK), Sept.2004
  - International Congress of Ecology (INTECOL-ESA), Montréal, Août 2005
  - Ecologie du Paysage (IALE France), Novembre 2005
- Vulgarisation (présentation et poster aux Doctoriales Bretagne)

VU :

Le Directeur de Thèse

Alain BUTET

VU :

Le responsable de l'Ecole Doctorale

VU pour autorisation de soutenance

RENNES, le

Le Président de l'Université de Rennes 1

Bertrand FORTIN

VU après soutenance pour autorisation de publication :

Le Président de Jury,

RESUME

Dans les dernières décennies, des modifications importantes sont apparues dans la structure et la composition des paysages agricoles, sous l'effet de changements dans les politiques et les méthodes de production de l'agriculture (mécanisation accrue, expansion des zones cultivées au détriment des habitats semi-naturels, augmentation de l'utilisation des intrants chimiques…). Face à tous ces changements liés à l'agriculture moderne, la question se pose de l'impact de l'intensification agricole sur la biodiversité.

Dans cette optique, nous nous sommes intéressés à une communauté de petits mammifères (rongeurs et insectivores < 40g) des haies dans trois paysages agricoles bretons contrastés du point de vue de l'intensité de l'usage des terres et de la densité des réseaux de haies, le long d'un gradient d'intensification de l'agriculture. Quatre axes principaux sont identifiés : (1) caractériser la structure et la composition de la communauté dans les trois paysages, (2) déterminer (dans une approche multi-échelle quelles sont les variables environnementales qui peuvent expliquer les différences dans les assemblages d'espèces entre les haies, (3) caractériser les variations saisonnières de la communauté et des populations qui la composent en réponse à la dynamique des paysages. (4) Nous nous sommes aussi intéressés à un niveau trophique supérieur en comparant les abondances de deux espèces de prédateurs des petits mammifères, la buse variable (*Buteo buteo*) et la faucon crécerelle (*Falco tinnunculus*) en réponse à la composition des paysages et à la disponibilité en proies.

Les résultats soulignent l'importance de développer des approches qui intègrent plusieurs niveaux d'organisation et plusieurs échelles d'analyse. La diversité, l'abondance, la composition, la biomasse et les amplitudes saisonnières de fluctuation de la communauté, ainsi que l'abondance des deux espèces de rapaces sont différentes entre les trois sites, montrant un effet de l'intensification de l'agriculture sur les différents taxons étudiés. Le paysage, mais également les caractéristiques de l'habitat sont impliqués dans la structuration des assemblages d'espèces.

Ces résultats permettent d'envisager des modes de gestion et d'aménagement pour la conservation de la biodiversité dans les paysages agricoles.

Mots clés *: écologie du paysage ; paysages agricoles ; petits mammifères ; rapaces ; hétérogénéité spatio-temporelle, éléments permanents*

ABSTRACT

During the last decades, drastic changes in farming landscape structure and composition have been induced by changes in agricultural production methods and policies (increase of machinery use, expansion of cultivated areas to the detriment of semi-natural habitats, growing use of chemical products….). A question increasingly associated with all these changes in modern agriculture is to known if there have been impacts of agricultural intensification on biodiversity.

In that way, we study a community of small mammals (rodents & insectivores < 40g) living in hedgerows, in three contrasted farming landscapes differing by their level of land-use intensity and hedgerow network density, giving an agricultural intensification gradient. The framework of the study is : (1) to characterize the composition and the structure of the community in the agricultural landscapes, (2) to identify (in a multi-scale approach) which environmental variables could be predominant for explaining differences in species assemblages between hedgerows, (3) to characterize seasonal variations of the community and component populations in response to landscape dynamics. (4) We also compare abundances of two small mammal predators, *Buteo buteo* and *Falco tinnunculus*, in response to the composition of the three sites, and to small mammal availability.

The results show the importance to develop an approach utilizing several organization levels and observation scales. Diversity, abundance, composition and biomass of the community, as well as abundance of the two raptor species, clearly differ between the study sites, showing an influence of agricultural intensification on the small mammal community and an higher trophic level. Both landscape and habitat scale are implied in structuring species assemblages. Seasonal patterns in the small mammal populations are the same whatever the site, but amplitude fluctuations are different, particularly for the dominant species.

These results could permit to propose action plans for the conservation of biodiversity in agricultural landscapes.

Keywords *: landscape ecology; farming landscapes; small mammals; raptors; spatio-temporal heterogeneity; permanent landscape elements;*